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1 **Systematic and locomotor diversification of the *Adapis* group (Primates,**
2 **Adapiformes) in the late Eocene of the Quercy (Southwest France) revealed by**
3 **humeral remains**

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17 climbing adaptations

18

19 **Abstract**

20 Twenty humeral specimens from the old and new Quercy collections attributed to the
21 fossil primates *Adapis* and *Palaeolemur* are described and analysed together. We

1 provide a qualitative and quantitative analysis of the different humeri, revealing that
2 high variability is present within the “*Adapis* group” sample. Six different morphotypes
3 are identified, confirming that what has often been called “*Adapis parisiensis*” is a mix
4 of different species that present different locomotor adaptations. Such a relatively high
5 level of locomotor diversity is unique in the Paleogene primate fossil record.

6 The humeral proportions of *Adapis* overlap with different groups of extant strepsirrhines
7 and platyrrhines depending on the specimen, so the popular view of *Adapis* as a loris-
8 like slow climbing primate does not apply to the whole sample presented here.

9 Moreover, different humeral features traditionally associated with “*Adapis parisiensis*”,
10 such as the absence of a zona conoidea and a reduced brachioradialis flange, are
11 variable depending on the sample studied. In addition, results of our analyses show that
12 adapine and omomyid humeral morphology overlap extensively, leading us to question
13 the accuracy of taxonomic attributions based on morphology of isolated humeri at
14 localities where omomyids and adapines of similar size coexist.

15 Finally, assuming our different morphotypes represent different species within two
16 genera, we propose a phylogenetic hypothesis relating these morphotypes, which
17 inhabited a small geographic area.

18 **Introduction**

19 Dental, cranial, and postcranial remains of the Eocene European primate *Adapis* were
20 found at the end of the nineteenth century, during the exploitation of phosphatic
21 deposits in the Quercy region, south-west France. It was evident to early researchers
22 that several species were represented in these “old Quercy collections”, represented by
23 material found in hundreds of fissure-fillings spread in the region (now dated from the
24 Middle Eocene to the late Oligocene). The old Quercy collections lack the information

1 of provenance of the fossils, and they represent numerous faunas coming from hundreds
2 of fissures (Legendre et al., 1997). However, since 1965, different teams from Paris,
3 Poitiers and Montpellier have organized field campaigns in the area and discovered new
4 fossils in well-identified karstic fillings, which are called “new Quercy collections”.
5 Among them are the localities of Rosières 2 and Escamps, which have yielded *Adapis*
6 material. The numerous new faunas accumulated in the Quercy have allowed many
7 systematic revisions of vertebrates. Among them, micromammals, especially the
8 abundant rodents, led researchers to propose a series of evolving specific lineages which
9 contributed to the elaboration of a regional biochronological scale. This work was used
10 for the elaboration of the European biochronological scale based on mammals, in which
11 Escamps is the reference fauna of the reference level MP 19. The distinction of several
12 levels (MP 17 – 20) in what were earlier considered Ludian faunas (Ludian is the latest
13 Eocene stage in the Paris Basin regional stratigraphy) was adopted following earlier
14 work on *Palaeotherium* lineages and the new studies of micromammals (Legendre,
15 1987). Reference faunas were chosen for their richness in both large and
16 micromammals. Complete faunal lists of all known Quercy localities were given in
17 Rémy et al. (1987). Rosières 1 to 4 were associated with four other localities as being
18 close to Escamps. Continuous work on Quercy faunas led to the introduction of a new
19 reference level MP 17b between the former MP 17a and MP 18 (BiochroM’97, 1997).
20 The use of numerical techniques underlined the proximity of MP 19 and MP 20, the last
21 Eocene level preceding the Grande Coupure (Terminal Eocene Event or TEE), and
22 suggested a probable small difference in age between Escamps and the slightly older
23 Rosières 2 (Escarguel et al., 1997). Since then, the revision of Quercy bats added to the
24 arguments differentiating MP 18 and MP 19 (likely lineage *Cuvierimops parisiensis*
25 *intermedius* – *C. p. parisiensis*), and also confirmed the identity of bats of several loci

1 within Escamps, which is a large fissure (Maitre, 2014). Updated faunal lists for
2 micromammals, with detailed references to all the original studies, are given by Sigé
3 and Hugueney (2006), comments on large mammals are given by Rémy and Sudre
4 (2006), and analyses of community structure and dynamics are given by Escarguel and
5 Legendre (2006). The progressive addition of new faunas, new systematic studies, and
6 technical advances, means that Rosières 2 now appears close in age to Escamps,
7 possibly slightly older, and both are placed in the latest Eocene, not far from the TEE.

8 *Adapis* species, too often considered as one species “*Adapis parisiensis*”, are adapiform
9 primates known from both cranial and postcranial remains (e.g., Delfortrie, 1873;
10 Filhol, 1882, 1883; Gregory, 1920; Gingerich, 1981; Gingerich and Martin, 1981;
11 Dagosto, 1983; Godinot, 1991; Bacon and Godinot, 1998; Godinot and Couette, 2008).
12 Stehlin (1912) added two species to the earlier named *A. parisiensis* and *Palaeolemur*
13 *betillei*, as a result of his study of well-preserved crania. Large-sized adapines have been
14 recently revised (Godinot and Couette, 2008), however the systematics of smaller-sized
15 adapines still needs clarification. At least four species can be distinguished among this
16 group (Lanèque, 1992, 1993; Godinot, 1998) based on cranio-dental remains from the
17 old Quercy collections. It has proven difficult until now to integrate this systematic
18 arrangement with the discoveries made more recently in well-identified localities
19 because the latter are represented by fragmentary remains (no crania found so far) and
20 adapine dentitions are quite uniform in morphology (Godinot, 1998, pers. obs.).

21 In the work that follows, the group of species of close size and morphology will be
22 referred to informally as the “*Adapis* group”. Postcranials have been ascribed to the
23 *Adapis* group since Filhol (1883) and Gregory (1920). More material coming from the
24 old collections was studied by Szalay and Dagosto (1980) and Dagosto (1983). This
25 material is often referred to “*A. parisiensis*”, however such a referral is misleading,

1 because there are many species represented in the *Adapis* group (Lanèque, 1992, 1993;
2 Godinot, 1998) and no one knows if the species *A. parisiensis*, described in the Paris
3 Basin, was really present in the Quercy or not. *Adapis* has traditionally been interpreted
4 as an arboreal quadruped with slow climbing adaptations and not a frequent leaper,
5 based on noted postcranial similarities to lorises. This loris-like slow climbing mode of
6 locomotion for *Adapis* was proposed by Dagosto (1983) due to several features of the
7 humerus such as the rounded humeral head that faces posteriorly, projecting proximal to
8 the tuberosities, the broad and shallow bicipital groove, the thick deltopectoral crest, the
9 well-marked and distally extensive tuberosity of teres major, the very large
10 brachioradialis flange extending proximally on the shaft, the absence of a distinct ridge
11 on the lateral side of the trochlea and the absence of a distinct groove between the
12 trochlea and the capitulum. Some of these features were also noted by Filhol (1882,
13 1883) as well as by Gregory (1920). However, some authors have suggested a more
14 “monkey-like” (i.e., pronograde arboreal quadruped) mode of locomotion for it
15 (Godinot and Jouffroy, 1984; Godinot, 1991; Bacon and Godinot, 1998).

16 Postcranials from both old and new Quercy collections have been attributed to *Adapis*.
17 When the new collections were recovered, researchers preserved information on the
18 local fissure for each bone. Furthermore, they processed sediments using screen-
19 washing techniques, yielding more small postcranials than in the nineteenth century
20 collections. Thanks to this, Godinot (1991) could compare closely the morphology of
21 two *Adapis* species coming from two distinct localities. One species from Rosières 2
22 appeared more quadrupedal and fast-moving, and the species from Escamps had traits
23 that suggested adaptations to climbing. A later study of femora and tibiae from both old
24 and new Quercy collections revealed that five different morphotypes could be
25 distinguished among the *Adapis* group femora, two of them being present at Rosières 2,

1 suggesting that an episode of locomotor diversification probably occurred in the *Adapis*
2 group (Bacon and Godinot, 1998). Field work in the Quercy continues, as well as
3 identification of specimens in the old collections, which are present in many
4 institutions.

5 Further study of the dental material from Rosières 2 indicated that at least two species
6 of *Adapis* were present in that locality, confirming the interpretation of the femora, and
7 providing a new perspective on the high morphological variability found earlier,
8 especially of the cuboid facet of *Adapis calcanei* of Rosières 2 and Escamps (Godinot,
9 1991). It also explained the variability in the humeri found in the same locality.

10 Here we present the study of several already-known and as yet undescribed humeral
11 specimens attributed to *Adapis* from old Quercy collections stored in several museums,
12 as well as specimens from new Quercy collections with a precise locality of origin. As
13 stated above, some *Adapis* humeri have been previously described and figured by Filhol
14 (1883), Gregory (1920), Szalay and Dagosto (1980), Dagosto (1983) and Godinot
15 (1991), but the whole sample has never been studied together. Only three complete
16 humeri, one proximal end and seven distal ends were available to Dagosto (1983), five
17 more distal ends were added by Godinot (1991), whereas now the total sample is up to
18 20 fossil remains.

19 Prosimian humeri of similar age are not very common in the fossil record. Concerning
20 adapiforms, the only humeri known besides those of *Adapis* are those of *Notharctus*
21 (Gregory, 1920), *Leptadapis* (Szalay and Dagosto, 1980), *Europolemur* (Franzen,
22 1987), *Protoadapis* (Godinot, 1994), *Pronycticebus* (Thalmann, 1994), *Cantius* (Gebo,
23 1987), *Adapoides* (Gebo et al., 2008), *Smilodectes* (Szalay and Dagosto, 1980),
24 *Darwinius* (Franzen et al., 2009), and asiadapids (Rose et al., 2009; Dunn et al., 2016).

1 Regarding omomyiforms, those of *Shoshonius* (Dagosto et al., 1999), *Necrolemur* and
2 *Microchoerus* (Dagosto, 1993), *Omomys* (Anemone and Covert, 2000), *Hemiacodon*
3 (Dagosto, 1993) and *Absarokius* (Covert and Hamrick, 1993) are known. Moreover,
4 early anthropoids of late Eocene age are also known from Egypt (Seiffert et al., 2000).

5 The primate humeri attributed to *Adapis* in the Quercy collections show a great
6 morphological and probably also taxonomic diversity. We hypothesize that these
7 primate humeri display morphological variability that is too great for a single species.
8 Even though it is not yet possible to make clear systematic attributions, we describe
9 them here as if they belonged to a series of morphotypes and discuss their possible
10 phylogenetic relationships. Regardless of the number of species, we test the hypothesis
11 that a loris-like slow-climbing morphology best fits these bones by analyzing
12 measurements of features known to provide information on locomotor behavior. Such
13 analysis could decipher the locomotor signal present in these humeri and tangentially
14 support the suggestion of multiple species if variation in the fossil sample overlaps that
15 of more than one locomotor group.

16 **Material and methods**

17 *Studied sample*

18 A total of 20 primate humeri have been identified from the old (10 specimens) and new
19 (another 10 specimens) Quercy collections. The latter set comes from the localities of
20 Rosières 2 and Escamps (Figs. 1- 6). Three are complete. Six are almost complete, only
21 lacking the humeral head and/or a small part of the distal epiphysis. Three are proximal
22 parts. Eight of them are distal parts. A complete list of all the specimens included in this
23 paper can be found in Table 1.

1 These bones are housed in different institutions: American Museum of Natural History
2 (AMNH, New York, United States of America), Muséum d'Histoire Naturelle Victor
3 Brun (MHNVB, Montauban, France), Muséum national d'Histoire naturelle (MNHN,
4 Paris, France), Université de Montpellier, Institut des Sciences de l'Évolution-
5 Montpellier (ISE-M, Montpellier, France), Aix-Marseille Université, Faculté des
6 Sciences Saint-Charles (FSM, Marseille, France), and the private collection of D.
7 Vidalenc (Vi, presently loaned to the MNHN in Paris, this collection will remain
8 available for study).

9 *3D surface reconstructions*

10 Most of the specimens studied herein were scanned from the original fossil using a
11 Breuckmann 3D surface scanner available at the “Plateau de morphométrie Outils et
12 Méthodes de la Systématique Intégrative, OMSI – UMS 2700 CNRS MNHN” of the
13 Muséum national d'Histoire naturelle (MNHN, Paris) with a medium lens. This surface
14 scanner allows the acquisition of the 3D surface of the bone at high resolution using
15 white light fringes (StereoSCAN^{3D} model with a camera resolution of five megapixels).
16 The specimens Ma-PhQ-330, Ma-PhQ-332, NMB-QW-1481 and AMNH-FM-10018
17 were scanned with the same scanner but this time using high quality casts instead of the
18 originals. Ma-PhQ-331 and Ma-PhQ-333 were not scanned but measured and
19 photographed at the MNHN in Paris.

20 All 3D surface reconstructions are available in the online repositories MorphoSource
21 (www.morphosource.org) and/or MorphoMuseum (www.morphomuseum.com; Marigó
22 et al., 2018). See Table 2 for information about 3D surface reconstructions, accessibility
23 and citation instructions.

24 *Nomenclature and measurements*

1 The anatomical terms used in the descriptions are illustrated in Figure 7. The
2 measurements taken are illustrated in Figure 8. Measurements were taken on the actual
3 bone when possible, using a digital caliper Electro DH (model 60.205), with a
4 resolution of 0.01 mm. When not possible, they were taken on the 3D reconstruction
5 using the 2D and 3D tools of the program Avizo (Visualization Sciences Group, 2009).
6 All measurements and indices taken can be found in Table 3. Measurements follow
7 Ford (1988), Szalay and Dagosto (1980) and Schmitt (1996). Indices of the proximal
8 ends follow Schmitt (1996), and those of the distal ends follow Szalay and Dagosto
9 (1980) and Boyer et al. (2010).

10 *Statistical analyses and descriptive indices and plots*

11 Univariate plots of proximal articular surfaces of humeri of extant and extinct primates
12 have been performed and are presented in Figure 9 (following Schmitt, 1996). Schmitt
13 (1996) calculated different indices that reflect locomotor behavior among living
14 strepsirrhines taking into account different measurements of the humeral head, and
15 found two that help distinguish between arboreal quadrupeds (AQ) and vertical clingers
16 and leapers (VCL): (1) the index of distal mediolateral width divided by central
17 proximodistal length of the humeral head (Fig. 8, 9A), and (2) the index of the height of
18 the humeral head derived from the distal mediolateral width divided by the distal
19 mediolateral width (Fig. 8, 9B).

20 The *Adapis* group sample is quite homogeneous regarding humeral head measurements,
21 but it presents a high variation in some measurements of the distal articulation (see
22 Table 3), which suggests that we may be dealing with more than one species in our
23 sample. In order to refute the hypothesis that our entire fossil sample can be treated as a
24 single population, we have performed a series of Levene's tests (Levene, 1960) on all

1 measurements of distal articulations in order to compare variances of two samples at a
2 time. In fact, we have compared the variance present in the *Adapis* group to the variance
3 in different species of living primates of similar size (*Saimiri sciureus*, *Hapalemur*
4 *griseus* and *Perodicticus potto*) as well as fossil primate specimens belonging to
5 different genera present in the Indian fossil site of Vastan Mine, the adapiform
6 *Marcgodinotius indicus*, the omomyiforms *Vastanomys gracilis* and *V. major*, as well as
7 at least one other unidentified euprimate from the same site. We collected data on seven
8 *S. sciureus*, 11 *H. griseus*, five *P. potto*, two *M. indicus*, one *V. gracilis*, one *V. major*
9 and four unidentified Vastan euprimate remains (see below for information on
10 comparative sample specimens). All Levene's tests have been performed using Excel,
11 calculating the mean of each of the groups (the *Adapis* group and the comparison
12 group), and then calculating the absolute value of the difference between each of the
13 original values and the mean value for the group. After these data transformations, a
14 one-way ANOVA has been performed, since its result is equivalent to the result of a
15 Levene's test.

16 Regarding the distal end of the humerus, Szalay and Dagosto (1980) found the
17 following two indices to be most informative in distinguishing locomotor behavior: the
18 trochlear articular index (TAI) and trochlear height-width index (THWI). These indices
19 (see results for *Adapis* in Table 3) have been traditionally used to distinguish between
20 AQ and VCL. We have calculated them for all *Adapis* specimens and compared them to
21 other primate taxa (see below for information on comparative sample specimens).

22 Because distal articulation indices were also found to be not very informative (see
23 Results section), we have performed principal components analyses (PCA) of four distal
24 humeral measurements: trochlear width (TW), maximum trochlear height (TH),
25 capitulum width (CW) and entepicondylar width (EEC). These results are presented in

1 Figure 10. See Figure 8 for information on how measurements were taken. Following
2 Boyer et al. (2010), measurements were size-standardized using geometric means, then
3 transformed into natural logarithms, and compared among taxa using PCA of the
4 Euclidean distance matrix relating the specimens using the software PAST (Hammer et
5 al., 2001).

6 For a complete list of taxa used as comparative samples for all statistical analyses,
7 indices and plots see Table 4.

8 **Results**

9 *Analyses of variance (Levene's tests)*

10 The *Adapis* group sample is quite homogeneous regarding humeral head measurements
11 (see Table 3), but it shows a significantly higher variance than any of the extant and
12 fossil species to which it has been compared in many measurements of the distal
13 articulation. Indeed, the presence and width of the zona conoidea shows significant (p -
14 value < 0.05) results when compared to *S. sciureus*, *H. griseus* and *P. potto*. Concerning
15 trochlear height, its variance in the *Adapis* group is also statistically different from that
16 of *S. sciureus* and *H. griseus*, and the total length of the humerus measured from below
17 the humeral head also significantly varies from that of *H. griseus* (see Table 5).

18 Moreover, indices concerning the distal articulation also show significantly greater
19 variance than in extant species. For instance, the TAI is significantly greater than in *S.*
20 *sciureus*, and the THWI index is significantly greater than in *H. griseus*. Indeed, the
21 extant specimens employed for the Levene's tests come from different institutions (see
22 Table 4), were collected in different locations and years, and they probably represent
23 different populations of the same species. Thus, significant results provide even stronger
24 support to the conclusion that the *Adapis* group specimens studied herein represent

1 multiple species. When the same data were compared to the fossil primates recovered
2 from Vastan Mine (India), belonging to at least two different genera and at least four
3 different species, and attributed to adapiforms and omomyids, the results are also
4 striking. We found that trochlear height and width of the zona conoidea were
5 significantly more variable in the *Adapis* group specimens than in the Vastan primates.

6 *Summary of the main features of each morphotype*

7 Due to the different morphological features found, we grouped the different specimens
8 into six morphotypes. A list of the different morphotypes and specimens included in
9 each one is given in Table 1. A complete table listing all features and specimens can be
10 found in SOM 1. Complete descriptions and comparisons of all the *Adapis* group
11 humeri studied in this paper arranged depending on morphotype attribution can be
12 found in SOM 2. For anatomical terms used see Figure 7.

13 Morphotype 1 specimens are characterized by being large and gracile, with a small
14 tubercle of teres major and a shallow bicipital groove, a laterally flaring brachioradialis
15 flange (except for specimen NMB-QW-1481, which has a straight brachioradialis
16 flange). Moreover, morphotype 1 specimens present a deep radial fossa and lack a zona
17 conoidea. Size and morphological differences between the complete humerus ISE-M-
18 ROS-2-95 and NMB-QW-1481 suggest that we place NMB-QW-1481 as aff. *sp.* 1.

19 Morphotype 2 specimens are medium to large with a medium robustness. They mainly
20 have, as all other specimens in this study do, a greater tuberosity below the level of the
21 humeral head, except for specimen Ma-PhQ-332 (*Adapis* cf. *sp.* 2), which has a greater
22 tuberosity that surpasses the humeral head slightly. They present a small tubercle of
23 teres major and a shallow bicipital groove, a straight or slightly concave brachioradialis

1 flange, a deep radial fossa (except for specimen Ma-PhQ-332, which is allocated to
2 *Adapis* cf. sp. 2), and present a zona conoidea.

3 Morphotype 3 specimens are medium to large in size and medium in robustness, and do
4 not have a prominent tubercle of teres major. They present a continuous crest between
5 the latter and the lesser tuberosity, and a deep bicipital groove. At the distal end,
6 morphotype 3 specimens present a straight brachioradialis flange and a deep radial fossa
7 (except for specimen FSM-PQ-1744, attributed to *Adapis* aff. sp. 3), and no zona
8 conoidea. Moreover, specimen MNHN-Qu-16583 presents the most rounded capitulum
9 and is attributed to *Adapis* cf. sp. 3).

10 The only morphotype 4 specimen is characterized by being small and robust, with a
11 prominent tubercle of teres major and a continuous crest present between the latter
12 tubercle and the lesser tuberosity, as well as a deep bicipital groove. At the distal end, it
13 presents a laterally flaring brachioradialis flange.

14 The only morphotype 5 specimen is very small and medium in robustness, with a
15 prominent tubercle of teres major but no crest connecting it with the lesser tuberosity,
16 and the shallowest bicipital groove of the whole sample studied herein. It is also
17 characterized by a straight (or even slightly concave) brachioradialis flange, a shallow
18 radial fossa and the lack of a zona conoidea.

19 Morphotype 6 specimens are large or medium-large in size and medium to gracile in
20 robustness. The prominence of their tubercle of teres major varies, but they all present a
21 continuous crest between that tubercle and the lesser tuberosity. Their bicipital grooves
22 are all medium to deep. Their distal ends present a laterally flaring brachioradialis
23 flange, a shallow radial fossa and the presence of a zona conoidea or at least a lateral lip
24 marking the lateral end of the trochlea.

1 Proximal articulation indices The indices found by Schmitt (1996) to reflect locomotor
2 behavior among living strepsirrhines, taking into account different measurements of the
3 humeral head, have been calculated for those *Adapis* specimens that preserve their
4 proximal epiphyses (Table 3, Fig. 9). See discussion of Figure 9 below with reference to
5 abbreviations for behavioral categories. We can see that in both graphs (Fig. 9) *Adapis*
6 specimens overlap with different species of arboreal quadrupeds (AQ) and vertical
7 clingers and leapers (VCL), although we can see some variation in the different
8 specimens. The mean of all *Adapis* specimens for the index of distal mediolateral width
9 divided by central proximodistal length of the humeral head (Fig. 9A) is equal to that of
10 the specimen MNHN-Qu-16584. However, the mean of all *Adapis* specimens for the
11 index of height of the humeral head derived from the distal mediolateral width divided
12 by the distal mediolateral width (Fig. 9B) does not overlap with any of the specimens
13 available. Figure 9A shows how VCLs have a narrower articular surface on the distal
14 third of the humeral head than AQs. Some *Adapis* specimens are closer to the VCL
15 means in this plot, suggesting a narrowing on the distal third of the humeral head in
16 these specimens. However, the specimen ISE-M-ROS-2-80 is closer to the AQ,
17 suggesting a wider distal third of the humeral head in this specimen. The range of
18 *Adapis* in this case is similar to those of *Notharctus* and *Smilodectes*, and mean and
19 standard deviation in the *Adapis* sample are below those of *Notharctus* and *Smilodectes*,
20 and further below those of *Cantius*. If we were interpreting these numbers in
21 comparison with the living strepsirrhine AQs and VCLs, we would have to conclude
22 that species of the *Adapis* group were more specialized leapers than notharctines, in
23 complete opposition with limb proportions or distal femur morphology, which clearly
24 show the absence of leaping specialization in the *Adapis* group (Dagosto, 1983). To
25 increase our understanding of these ratios, we calculated them in platyrrhines showing

1 different kinds of locomotor adaptations, and also in some lorises (Fig. 9). Few
2 differences appear among the platyrrhines, and in fact the most contrasted results are
3 between *Adapis* species and lorises. It seems that this ratio conveys a strong
4 phylogenetic signal, and is difficult to simply interpret in terms of locomotion. In fact,
5 the range of *Adapis* specimens overlaps with all locomotor categories in Figure 9A.
6 This strengthens the assertion that this index (ML/PD values) is minimally useful in
7 distinguishing between locomotor groups.

8 The other ratio quantified by Schmitt (1996) among living strepsirrhines (Fig. 9B)
9 shows that VCLs present a higher distal third of the humeral head compared to AOs.
10 *Adapis* in this case falls in between AO and VCL, and its mean is very close to that of
11 *Haplemur griseus*. The most “quadrupedal” specimens of *Adapis* are ISE-M-ROS-2-
12 80 and ISE-M-ROS-2-95, which present a lower distal third of the humeral articular
13 surface than the rest of the specimens. If we compared this index directly between
14 *Adapis* and notharctines, it would suggest that *Adapis* species had less leaping
15 tendencies than *Notharctus* and most *Smilodectes*, but still clearly more leaping
16 propensities than *Cantius* species, which is likely not the case. Taking into account our
17 broader sample of living taxa, we can see that all platyrrhines present a quite high distal
18 third of the humeral head (higher than in most VCLs), and much higher than
19 strepsirrhine AOs. We see more variation in this index within platyrrhines, with *Ateles*,
20 *Pithecia*, *Aotus* and *Saimiri* presenting higher distal thirds of the humeral head than
21 *Cebus* and particularly *Alouatta*. *Adapis* mainly overlaps with *Alouatta* in this regard,
22 and this might be a real functional signal, as *Adapis* has been interpreted as a relatively
23 slow moving primate (Dagosto, 1983). It might well have had a deliberate kind of
24 quadrupedalism, as is typical of *Alouatta*. Here again, a noticeable fact is that *Adapis*
25 species appear far away from living lorises, suggesting that the interpretation of them

1 as slow climbers (Dagosto, 1983) has to be corrected in favor of a less specialized kind
2 of quadrupedalism (Godinot, 1991). However, these conclusions have to be considered
3 provisional, as it is again clear that this ratio also includes a strong phylogenetic signal.
4 It is in fact remarkable how different strepsirrhine AQs are from platyrrhine AQs,
5 suggesting that platyrrhines do not share the same adaptations as strepsirrhines
6 concerning humeral head shape associated with locomotor behavior, or that it is
7 inappropriate (from a mechanical and behavioral perspective) to consider strepsirrhine
8 AQs as equivalent to platyrrhines. That is, they inhabit very different environments that
9 likely put different locomotor pressures on them. This same pattern has also been seen
10 in other bones such as the calcaneus and the femur (Bacon and Godinot, 1998).

11 Distal articulation indices The trochlear articular index (TAI) is generally high in
12 arboreal quadrupeds (AQs) and low in vertical clingers and leapers (VCLs). Contrarily,
13 the trochlear height-width index (THWI) is usually high in VCLs and low in AQs
14 (Szalay and Dagosto, 1980). The results for different *Adapis* humeri when these indices
15 are calculated for each of them are listed in Table 3, together with the definition of these
16 indices. The values that represent the different specimens are strikingly different (see
17 Table 3 and SOM 3).

18 The TAI indicates the relative portion of the articular width occupied by the trochlea in
19 anterior view. Most of the *Adapis* specimens studied here are close to the 40% that
20 Szalay and Dagosto (1980) calculated for adapiforms. However, the specimen FSM-
21 PQ-1744 falls far above the 40%, indicating the presence of a proportionally wider
22 trochlea, which makes it fall closer to microchoerine omomyids, and also close to
23 *Eulemur mongoz* and *Lemur catta*. We must note that the indices provided by Szalay
24 and Dagosto (1980) are not exactly the same as the ones we obtained for the same
25 specimens, NMB-QW-1481 and AMNH-FM-10018 (specimen that the former authors

1 mistakenly called AMNH-FM-81001). Szalay and Dagosto (1980) mentioned in their
2 work the difficulty of replicating accurately some of these measurements.

3 The THWI indicates the relationship between the height and width of the anterior side
4 of the trochlea. In extant quadrupedal primates, the trochlea is wider than high as in
5 most *Adapis* specimens (index less than 100). However, extant VCL taxa present an
6 index higher than 100 because of the secondarily shortened trochlea and/or the increase
7 of joint surface area on the anterior side of the humerus (Szalay and Dagosto, 1980).

8 Only one of the specimens studied presents an index much higher than the other
9 specimens and closer to 100 (Vi-Esc--839). This specimen presents an anterior side of
10 the trochlea that is closer in height to the capitulum, whereas for the rest of the *Adapis*
11 group sample studied here the trochlea is always much lower than the capitulum in
12 height. The only other specimen from the same site (ISE-M-ECA-1364) is missing the
13 capitulum, but the trochlea, even if not as high as in Vi-Esc--839, still appears higher
14 than in other *Adapis* group specimens. The variability found in the *Adapis* group for this
15 index clearly surpasses that found in extant *Hapalemur griseus* (see Table 5). Moreover,
16 taking into account that trochlear height is one of the variables for which we also
17 obtained significant results of extremely high variance in the *Adapis* group, this
18 supports the idea that these specimens probably represent a different species (our
19 morphotype 3).

20 In addition, if we look at the values obtained for the different morphotypes, they vary
21 within each morphotype. Within morphotype 3, FSM-PQ-1744 has peculiar values.
22 However the other two, Vi-Esc-839 and MNHN-Qu-16583 have values similar to those
23 of other morphotypes. Ma-PhQ-330 is peculiar in the other direction, however the other
24 specimen from morphotype 6, MNHN-Qu-16584, again has values similar to those of
25 other morphotypes. The group from Rosières 2 + NMB-QW-1481 (morphotypes 1 and

1 2) might seem more homogeneous, however in fact Ma-PhQ-332, placed with the
2 morphotype 2 from Rosières 2, again has different values. It appears that the variation
3 within morphotypes is relatively large, and that the values from the different
4 morphotypes largely overlap with each other. In sum, the numbers found for the indices
5 TAI and RTWI (Relative trochlear width index, see Table 3) do not allow the
6 differentiation, morphological or functional, of morphotypes. However, the generally
7 low THWI indices in the *Adapis* group are opposite to the high values of VCLs and
8 especially slow climbers (see values in SOM 3), very probably giving them a real
9 functional signal of broadly arboreal quadruped types of locomotion.

10 *Principal components Analysis*

11 The results of the PCA of some distal humeral measurements can be found in Figure 10.
12 There is no overlap of the *Adapis* fossils with Plesiadapidae, Lorisidae and Tarsiidae
13 (Fig. 10A). In Figure 10B we show the results of the same analysis only including fossil
14 forms as well as extant strepsirrhines and tarsiers. However, we can see that the results
15 from both analyses are not very different in terms of overlapping morphospace.

16 PC1 is mainly driven by increasing entepicondylar width (EEC), and PC2 is mainly
17 driven by increasing trochlear height (TH) and decreasing trochlear width (TW). In both
18 plots, a number of *Adapis* group specimens overlap with omomyids and especially
19 microchoerines, and, depending on the specimen, overlap with extant strepsirrhines
20 and/or platyrrhines. The large area covered by the *Adapis* group is again a testimony of
21 its unusual morphological diversity when compared to extant groups.

22 Of the 15 *Adapis* group specimens available, seven clearly overlap with proportions
23 circumscribed by omomyids and none of them overlaps with plesiadapiforms.

1 Moreover, there is no overlap between *Adapis* group specimens and lorisids whatsoever
2 regarding distal humeral morphospace (Figure 10A and 10B)
3 Esc 839 overlaps with the morphospace of Pitheciinae, but it does not overlap with any
4 extant strepsirrhine group, FSM-PQ-1744 overlaps with Galagidae, NMB-QW-1481
5 overlaps with Callitrichinae and Galagidae, and Ma-PhQ-330, MNHN-Qu-16584, ISE-
6 M-ROS-2-95 and MNHN-Qu-16583 overlap with Omomyidae. Specimen Vi-Ros-640
7 and Ma-PhQ-332 do not overlap with any other group but they fall very close to
8 Omomyidae, Galagidae and Callitrichinae.
9 Vastan primates have also been included in the PCA, as well as the fossils *Smilodectes*
10 and *Notharctus* (Figure 10A and 10B). *Smilodectes* overlaps only with Atelinae, and
11 also falls close to some Indriidae. *Notharctus* specimens, on the other hand, fall closer
12 in morphospace to Plesiadapidae than to the *Adapis* group. Specimen AMNH-FM-
13 127167 does not overlap with any fossil or extant group, and specimen USNM 21864
14 overlaps with both Omomyidae and Plesiadapidae (Figure 10A and 10B).
15 Regarding Vastan primates, at least four different species have been identified (see Rose
16 et al., 2009 and Dunn et al., 2016). One form, attributed to an unknown euprimate, is
17 represented here by specimens GU 713, GU 765 and GU 9005. The first specimen falls
18 very close to the morphospace occupied by Lorisidae, and very close to *Hapalemur*
19 *simus* as well, far from the *Adapis* morphospace, the second one overlaps with the
20 common morphospace of omomyids and *Plesiadapis* (overlapping with microchoerine
21 omomyid number 4 [M4 in Figure 10B]), and the latter falls in between the
22 morphospace occupied by *Notharctus* and *Smilodectes* but closer to the latter, and also
23 closer to Plesiadapidae and Tarsiidae than to Lorisidae. Another form, attributed to the
24 adapiform *Marcgodinotius indicus*, is represented by specimens GU 763 and GU 812.
25 The former overlaps with Galagidae in morphospace, and the latter overlaps with

1 Atelinae and falls in between the morphospace occupied by Plesiadapidae and
2 Tarsiidae. On the other hand, the specimens attributed to the omomyid *Vastanomys* (GU
3 764 and GU 1692) overlap with Omomyidae, but both fall very close to the
4 morphospace occupied by the *Adapis* group, the former also falling very close to
5 *Lepilemur mustelinus*, and the latter specimen (*V. major*) also falling very close to the
6 *Adapis* group specimen MNHN-Qu-16583 (morphotype 3).

7 To summarize, *Adapis* group specimens show a great variability concerning distal
8 epiphyseal measurements, overlapping with many primate groups, including
9 platyrrhines. Some specimens overlap mostly with omomyids, again suggesting that
10 differences between adapiforms and omomyiforms are not so clear regarding distal
11 humeral proportions.

12 **Discussion**

13 *Number of species*

14 From the morphological variation present in the *Adapis* humeri studied in this work, we
15 have concluded that six different morphotypes, probably corresponding to at least six
16 different species, are present. A summary of the different morphotypes observed and the
17 specimens attributed to each one is presented in Table 1. In SOM 1, we provide a
18 summary of the different features observed in every specimen studied, while complete
19 descriptions can be found in SOM 2.

20 As seen in the statistical analyses used, some features of the distal articulations of the
21 *Adapis* group present higher variance than in extant species of similar size, as well as
22 the same variance as adapiforms and omomyids found in the same fossil site (Vastan
23 Mine) in India (Table 5). The differences in length and overall proportions of the
24 different humeri, the width (presence or absence) of the zona conoidea and trochlear

1 height in the sample studied confirm that more than one species (and probably more
2 than one genus) is present in our sample.

3 *Functional morphology and locomotor behavior*

4 The humeral shafts of all the *Adapis* group humeri are retroflexed, with the humeral
5 heads more posterior than the shaft and the humeral heads are flattened posteriorly, as
6 happens in generalized arboreal quadrupedal primates (Gebo, 2014). The greater
7 tubercle is generally slightly lower than the humeral head except for one specimen (Ma-
8 PhQ-332), which presents a greater tubercle slightly above the humeral head, which
9 happens in lemurs, most platyrrhines and some colobines (Gebo, 2014). In this regard,
10 the *Adapis* group humeri appear similar to living active arboreal quadrupeds, which
11 present humeral tuberosities of roughly the same height as the humeral head (Jolly,
12 1967; Gebo, 1988; Rose, 1988; Harrison, 1989; Kay, 2005).

13 As previously discussed, all the humeral heads in the sample present similar proportions
14 of the whole head and the articular surface area, with all specimens having similar
15 length and width measurements of the head, and all specimens presenting a slightly
16 longer than wide humeral head. Ma-PhQ-332 (the specimen with the highest greater
17 tuberosity) is also the specimen with the longest humeral head relative to width. Even
18 though no significant features are found regarding the proximal articulation that could
19 indicate important differences in locomotor behavior, our measurements indicate a
20 generalized type of locomotion, with no specific specialization for vertical clinging or
21 leaping or slow climbing (Figures 6A and 6B). In fact, the humeral heads of the *Adapis*
22 group specimens do not present the strikingly rounded humeral head of lorisisds (see
23 Figure 11).

1 On the contrary, the distal ends of the humeri of the *Adapis* group specimens studied
2 herein present significant differences depending on the different morphotypes discussed,
3 especially in some features such as the development of the brachioradialis flange, the
4 height of the trochlea, and the presence of a zona conoidea.

5 The striking variability we find in the development of the brachioradialis flange of the
6 different *Adapis* specimens could indicate differences in locomotor behavior (Fabre et
7 al., 2017). Adapiforms usually present an extensive development of the brachioradialis
8 flange (Gregory, 1920; Dagosto, 1983; Gebo, 2014), which has been interpreted as
9 being an indicator of better-developed arm muscles when compared to those of extant
10 strepsirrhines. The rounded brachioradialis flange offers a large attachment surface for
11 the muscles brachioradialis, brachialis and triceps brachii (Jouffroy, 1962). Thus, we
12 could hypothesize that those *Adapis* presenting more laterally expanded brachioradialis
13 flanges must possess larger flexion and extension muscles in the elbow joint, resulting
14 in more powerful flexion and extension of the forearm. The triceps muscle (extensor of
15 the elbow joint) is essential for climbing on highly inclined supports, and brachialis and
16 brachioradialis muscles are the main flexors of the forearm and used in fast flexions of
17 the forearm, as well as slow flexions against resistance, no matter the position of the
18 hand (Basmajian and Latif, 1957). This could indicate that those specimens presenting
19 larger brachioradialis flanges (especially morphotypes 4 and 6) present some vertical
20 climbing component in their locomotion.

21 However, even though having those more powerful muscles should indicate changes in
22 locomotion, we find massive brachioradialis flanges in extant taxa that have very
23 different locomotor repertoires such as *Daubentonia*, *Microcebus* and *Lepilemur*, and
24 narrow and straight flanges in indriids as well as *Loris* and *Nycticebus*, though lorids
25 such as *Perodicticus* present an intermediate flange development (see Figure 11) closer

1 to *Varecia* or *Lemur*. The effects of having larger, smaller, straighter or more curved
2 brachioradialis flanges are not clear and should be further explored. A well developed
3 brachioradialis flange, however, is also present in plesiadapiforms, omomyids (see
4 Figure 11) and microchoerids (Szalay and Dagosto, 1980). This broad distribution has
5 led to the idea that a large crest is primitive for primates. Since a flexed position of the
6 forelimb is primitive for mammals (Jenkins, 1971), this flange tends to decrease in
7 development in many primates as the forelimb becomes less habitually flexed. A long
8 brachioradialis flange is no doubt linked to a position with flexed limbs during
9 locomotion.

10 The *Adapis* specimens described in this work have different degrees of development of
11 the brachioradialis flange. However, they never reach the exceptional development
12 observed in *Leptadapis* (Szalay and Dagosto, 1980; see Figure 11). A proximally
13 extensive brachioradialis flange has been discussed to be more typical of adapoids than
14 omomyids (Gregory, 1920; Dagosto, 1983). However, some microchoerines present
15 highly developed flanges (Szalay and Dagosto, 1980).

16 Traditionally, the humerus of *Adapis* has been considered to present a quite reduced
17 brachioradialis flange and no zona conoidea on its distal end, based on a single
18 specimen attributed to *A. parisiensis* (Gebo et al., 2007). Szalay and Delson (1979)
19 suggested that the development of the brachioradialis flange in *Adapis* was quite small
20 and that it approached the reduced condition seen in most platyrrhines. However, we see
21 in the sample analyzed here that this is not always the case. We see several specimens
22 with relatively large brachioradialis flanges (ISE-M-ROS-2-95, MNHN-ACQ-262,
23 MNHN-Qu-16584, Ma-PhQ-331, Ma-PhQ-333, ISE-M-ROS-2-534: morphotypes 1, 2,
24 4 and 6), and we also see specimens that present a clear separation between the trochlea
25 and the capitulum (Ma-PhQ-332, Ma-PhQ-330, ISE-M-ROS-2-79, Vi-Ros-640:

1 morphotypes 2 and 6). All these specimens do not fall in the “traditional” *Adapis*
2 morphotype and in fact show a remarkable diversity of morphologies within the *Adapis*
3 group.

4 The entepicondylar foramen is a primitive feature found in primitive mammals that
5 serves as a passage for the median nerve and the brachial artery when it is present
6 (Landry, 1958). It can be found in many fossil primates as well as most living
7 prosimians, some platyrrhines, and is exceptionally present in *Homo* (Ankel-Simons,
8 2007). Variation in the size and shape of this foramen within the same species is
9 sometimes observed (Landry, 1958), however the differences found among *Adapis*
10 specimens are quite large and could well convey a phylogenetic signal: the very large
11 entepicondylar foramen of AMNH-FM-10018 could indicate that our morphotype 5 is
12 more primitive than the others; and conversely, the very small entepicondylar foramen
13 of MNHN-ACQ-262, which is in a state of advanced reduction, may well indicate an
14 advanced evolutionary stage for our morphotype 4. ISE-M-ECA-1364 also has a small
15 entepicondylar foramen possibly indicating an ongoing reduction of the foramen in the
16 Escamps species (morphotype 3).

17 Our morphotype 3 specimens also present the tallest trochleas (relative to width).
18 Moreover, our Levene’s test results support the idea that such differences in trochlear
19 height in the different *Adapis* group specimens is higher than in extant species of similar
20 size and higher than those seen in Vastan Mine primates attributed to different genera.
21 The same is true in some cases for the THWI index. Specifically, specimen Vi-Esc-839
22 presents an anterior side of the trochlea that is closer in height to the capitulum, whereas
23 for the rest of the *Adapis* sample studied here the trochlea is always much lower than
24 the capitulum in height. The only other specimen from the same site (ISE-M-ECA-
25 1364) is missing the capitulum, but the trochlea, even if not as high as in Esc 839, still

1 appears higher than in the other *Adapis* specimens. We interpret the high trochlea as a
2 derived trait that must have appeared in one *Adapis* lineage. *Smilodectes* (an adapiform
3 inferred as a VCL) and other VCLs also present particularly high THWI indices,
4 however VCL seems extremely unlikely in the Escamps species. Among the tarsals of
5 the Escamps *Adapis* described by Godinot (1991), the astragali with a very flat trochlea
6 clearly indicate a mobile upper ankle joint, and one tibia and several femora from
7 Escamps studied by Bacon and Godinot (1998) also reflect a high mobility at the level
8 of hip, knee and ankle joints. In this context, the high THWI index of these specimens is
9 to be compared to the high index of lorises, indicating the frequent use of highly flexed
10 forearms in the context of a climbing adaptation.

11 Our results for distal articulation indices present values for *Adapis* group specimens that
12 are closer to those obtained for omomyids than for lorises. This suggests that these
13 values are indicating a generalized quadrupedalism behavior, which contrasts not only
14 with VCL but also with the locomotion of living lorises. Moreover, no specimens of
15 the *Adapis* group present the relative increase in size of the capitulum typical of lorises
16 (Gebo et al., 2007; Figure 11).

17 The high variability shown in these indices in the different *Adapis* group specimens
18 present within the sample studied here strongly agree with the idea that several species
19 must be represented within this sample, or even several genera, if we take into account
20 that no differences in variance were found between the specimens attributed to the
21 *Adapis* group and Vastan Mine primates which belong to at least four species of both
22 adapiforms and omomyids. From the study of femora and tibiae, Bacon and Godinot
23 (1998) distinguished five locomotor types probably reflecting at least five species, and
24 suggested that probably two genera (*Adapis* and *Palaeolemur*) were present. From the
25 humeri, we can see even more diversity, with six morphotypes, and our morphotype 6

1 being quite heterogeneous and probably representing more than one species. Despite
2 this variability, the relatively low THWI found for most of the *Adapis* group specimens
3 makes them similar to living arboreal quadrupeds routinely using moderately flexed
4 forearms, and emphatically different from VCL and slow climbers which frequently
5 strongly flex their forearms.

6 The three specimens that have both the proximal articular surface and the distal articular
7 surface preserved (MNHN-Qu-16584, ISE-M-ROS-2-95 and Ma-PhQ-332), present
8 similar proportions of the humeral head, presenting a similar width of the distal third of
9 the humeral head (Figure 9A). The heights of the distal third of the humeral head are
10 different, but all are within the range of *Hapalemur griseus* (Figure 9B), ISE-M-ROS-2-
11 95 being the specimen with the lowest distal third of the humeral head, and MNHN-Qu-
12 16584 one of the *Adapis* specimens with the highest distal third of the humeral head.
13 Ma-PhQ-332 is very close to the mean for *Adapis*. These results could indicate that
14 MNHN-Qu-16584 is a little more leaping specialized than the rest of the specimens
15 represented by proximal articular surfaces, since a higher head has been associated with
16 a stronger leaping component (Schmitt, 1996). However, VCLs also present a narrow
17 head and this specimen does not have the narrowest humeral head of the whole *Adapis*
18 sample (see Figure 9).

19 Regarding distal articulation proportions, our PCA results show that two out of these
20 three specimens (MNHN-Qu-16584 and Ma-PhQ-332) overlap with omomyids (Fig.
21 10), suggesting that omomyids and adapiforms were not very different in distal humeral
22 proportions. Moreover, our results of the Levene's tests comparing the *Adapis* group
23 with Vastan Mine primates also confirm this hypothesis. On the other hand, Ma-PhQ-
24 332 falls very close to *Otolemur crassicaudatus*. The morphospace occupied by the
25 Callitrichinae regarding distal humeral proportions falls right in the middle of the

1 *Adapis* morphospace. This could suggest that some galagids as well as some
2 platyrrhines might be a better model for understanding distal humeral morphology of
3 the extinct *Adapis* rather than lorises.

4 In summary, our PCA results again make it evident that distal humeral proportions of
5 strepsirrhines and haplorhines had many things in common in early forms, and that
6 telling them apart is not as easy as previously thought. In any case our study has two
7 clear conclusions. First it confirms the extraordinary morphological diversity found
8 within the *Adapis* group. Second, despite the partial overlap of the group with many
9 strepsirrhines and omomyids, the absence of overlap with lorises is important,
10 suggesting that species of the *Adapis* group may not have shared the specializations of
11 living lorises.

12 *Hypotheses of phylogenetic relationships and functional interpretations*

13 Before exploring the possible phylogenetic relationships of the different morphotypes, it
14 is important to recall what the general “*Adapis* pattern” may be. Earlier studies found
15 that these species have no characters recalling living VCLs (Dagosto, 1983; Godinot,
16 1991; Bacon and Godinot, 1998). They have no lengthening of the hindlimb, no leaping
17 characters on the distal femur or on the tarsals. This is confirmed by the general
18 appearance of their humeri. Placed side to side with a humerus of *Smilodectes* (a
19 Paleogene adapiform inferred to be a VCL; see Figure 11) with a similar shaft size, the
20 latter appears to have a proportionally smaller, narrower and more anteroposteriorly
21 elongated articular head, and also a more proximally salient articular head as in living
22 indriids. The general appearance of these *Adapis* humeri confirms that VCL is not
23 possible for them. On the other hand, since Dagosta’s (1983) study *Adapis* has often
24 been compared with lorises, however all indices, proportions, qualitative characters

1 and, especially, multivariate analyses of these humeri have shown that they are
2 distinctly different from our sample of lorisisids. The latter have, for example, a strongly
3 proximally salient articular head, linked to their high shoulder mobility, which is not
4 ever present in the *Adapis* group. Species of *Adapis* pertain to a broad category of
5 arboreal quadrupeds, some of which may have had relatively deliberate kinds of
6 locomotion, but none of which shared the articular specializations linked to the cryptic
7 adaptation of living slow climbers (Godinot and Jouffroy, 1984; Godinot, 1991; in
8 partial accordance with Dagosto, 1983).

9 If we try to make sense of the differences found between the different morphotypes, one
10 group is clearly separated from all the others, the group uniting morphotypes 3 and 5.

11 The humeri of this group differ by a shorter proximal part: whereas in all the others, the
12 deltopectoral crest extends around half way distally along the shaft, MNHN-Qu-16583
13 and AMNH-FM-10018 have a much shorter deltopectoral crest, giving them a very
14 different profile (Figs. 3 and 5 respectively). Associated with this is a straighter shaft,
15 less anteroposteriorly narrow, and the proximal surface for the unfused articular head
16 suggests that the latter was less posteriorly directed than in the other morphotypes.

17 Distally, the brachioradialis flange is straight, the medial epicondyle is much less salient
18 both medially and distally than in the other morphotypes, and they possess the most
19 spherical and salient capitulum. Such marked differences suggest that these two
20 morphotypes had a general increased agility in comparison with all the others.

21 Morphotype 3 includes the two Escamps specimens, with Vi-Esc-839 which appeared
22 quite specialized on the PCA diagram. Morphotype 3 was found to present the most
23 features associated with climbing among the five morphotypes, which from the
24 morphology of femora and tibiae were delineated in a spectrum from more quadrupedal
25 to more climbing forms (Bacon and Godinot, 1998). Concerning tarsals, the astragali

1 and calcanei from Escamps also indicated a much more mobile foot than in the species
2 from Rosières 2, again suggesting a great agility in climbing in this species (Godinot,
3 1991). The two localities Rosières 2 and Escamps are considered to be latest Eocene,
4 just prior to rapid extinction in Europe, and their different species indicate a diversity
5 of at least three subcontemporaneous species. The species from Escamps, morphotype
6 3, appears to be the most specialized in terms of agility and climbing among the whole
7 *Adapis* group. The species from Escamps may be close to *Palaeolemur betillei* from the
8 old Quercy collections (Bacon and Godinot, 1998), however this attribution must await
9 confirmation from further dental studies. Given the biochronological context,
10 morphotype 5 is very probably older, and in fact it appears as a likely ancestral form for
11 morphotype 3, with its smaller size and larger entepicondylar foramen. Other small
12 differences between them are less easy to interpret, AMNH-FM-10018 having a more
13 proximally located teres major tubercle, distally a deeper trochlear concavity (ulna
14 better stabilized on the humerus). The shallower olecranon fossa in AMNH-FM-10018,
15 reflecting less forearm extension in this ancestral form, would fit with the hypothesis of
16 an increase in the capacity of forearm extension in the lineage, consistent with the
17 extremes of hindlimb mobility found in the Escamps species.

18 The other four morphotypes generally show more anteroposteriorly compressed shafts,
19 more posteriorly inclined proximal articular heads, and a combination of more extensive
20 muscular insertions (longer deltopectoral crests and often more salient brachioradialis
21 flanges), more salient medial epicondyles and somewhat less mobile elbows. They
22 would indicate more generalist and powerful active arboreal quadrupeds. Among them,
23 morphotypes 1 and 2, present at Rosières 2 and sharing several characters, may
24 represent the most quadrupedal end of the spectrum, as was found by Bacon and
25 Godinot (1998) when studying hindlimb bones, which are easier to interpret

1 functionally. Their brachioradialis flanges are less extended than in morphotype 6. The
2 capitulum is slightly keeled anteroposteriorly on Vi-Ros-640 and ISE-M-ROS-2-79,
3 which may reflect predominantly anteroposterior movements. Several of these humeri
4 show the best developed dorsoepitrochlear fossae, indicating that the elbows were not
5 only less mobile in pronation-supination (less spherical capitulum) but also tightly
6 maintained by strong ligaments. These morphotypes seem to be interpretable as active,
7 possibly rapidly moving, arboreal quadrupeds. They seem to indicate a lineage (with
8 two species at Rosières 2) with increased quadrupedal specialization at the end of the
9 Eocene. Were they walking and running, maybe more horizontally jumping, on
10 branches? A specimen like Ma-PhQ-332 also has a greater tuberosity higher than the
11 articular head and distally the largest dorsoepitrochlear fossa: could a restricted shoulder
12 mobility associated with a ligamentous reinforcement of the elbow suggest a first
13 degree of semi-terrestriality? Interpreting differences between them, probably between
14 different closely related species, would need more abundant and better preserved
15 specimens. In any case, these latest Eocene morphotypes together strongly suggest a
16 second line of specialization in the *Adapis* group, toward more specialized
17 quadrupedalism.

18 Morphotype 6 is a heterogeneous group, representing between two and four different
19 species, that we consider probably primitive for the second group (morphotypes 1, 2, 4
20 and 6), especially because they have more extended brachioradialis flanges. Ma-PhQ-
21 333 is the most gracile and has a very large entepicondylar foramen. It could well be the
22 most primitive in this group. Its slightly less distally extended deltopectoral crest recalls
23 the other group (morphotypes 3 and 5) and might suggest either closeness to their
24 common origin or an early convergence. It is difficult to comment more on these bones
25 because they are incomplete. Only MNHN-Qu-15584 is complete and seems to belong

1 to a powerful arboreal quadruped. Morphotype 4 is a special case, represented by one
2 specimen, MNHN-ACQ-262. It belongs to the same large group, however it presents
3 some characters shared with morphotypes 1 and 2, and several autapomorphic
4 characters, like the prominent deltopectoral crest, the deep olecranon fossa and the
5 presence of a crest between the lesser tuberosity and the tubercle of teres major. This
6 suggests that it represents a “side-specialization” branched off from the broad line of
7 evolution going from the primitive group (morphotype 6) to morphotypes 1 and 2. On
8 the whole, we propose a schema of four evolutionary lines, one represented by
9 morphotypes 5 to 3, the others branched off from the primitive morphotype 6 and
10 having evolved toward morphotype 4 and toward morphotypes 1 and 2.

11 The great diversity present in the *Adapis* group poses a problem for the performance of
12 phylogenetic analyses of primates containing *Adapis parisiensis* from now on, since
13 what has been traditionally called *A. parisiensis* is most probably constituted of
14 different species. Common character matrices used for phylogenetic analyses (Seiffert
15 et al., 2005, 2009; Marigó et al., 2011, 2013, 2016; Femenias-Gual et al., 2017a,b)
16 contain codifications of humeral features such as the brachioradialis flange (usually
17 coded as moderate to large for *A. parisiensis*), the trochlear-capitular junction (usually
18 coded as confluent), and the relative width of the capitulum, which may need to be re-
19 coded in future analyses in order to include all the character states present in the *Adapis*
20 group sample. Indeed, exchanging “*Adapis parisiensis*” for “*Adapis* group” would be
21 better in future phylogenetic analyses using postcranial characters in order to illustrate
22 that *A. parisiensis* is most probably in this case a compilation of different closely related
23 species or even closely related genera. In fact, that several species of *Adapis* are
24 recongnized through cranial characters has been known for a long time (Stehlin, 1912;
25 Lanèque, 1992, 1993).

1 **Conclusions**

2 The primate humeri attributed to *Adapis parisiensis* in the Quercy collections show a
3 great morphological diversity, with variance in some features of the distal articulation
4 exceeding that found in living species, confirming the hypothesis that several species
5 must be represented within the sample, as has been proposed in previous studies of the
6 femora and tibiae. Even though it is not yet possible to make clear systematic
7 attributions, six different morphotypes are described, probably corresponding to at least
8 six different species.

9 Humeral features previously thought to be not present in *Adapis*, such as the zona
10 conoidea, are shown to be variable, since they are present in some specimens attributed
11 to the *Adapis* group. Moreover, this is one of the features that has been shown to have
12 much less variance in extant species. This high morphological variability suggests that
13 locomotor diversification occurred among this group and that different locomotor
14 repertoires were used by different species (or morphotypes).

15 Two clear groups can be distinguished in the sample, one including morphotypes 3 and
16 5, and a second one including morphotypes 1, 2, 4 and 6. Regarding the former,
17 morphotype 5 is probably older and it is probably ancestral to morphotype 3, which
18 appears specialized towards agility and climbing adaptations, and may include
19 specimens of the genus *Palaeolemur*. In the latter group, we find more generalist active
20 arboreal quadrupeds. The idea that modern lorises are analogous to fossil adapines finds
21 no support from examination of the humerus. *Adapis* group specimens do not overlap
22 with living lorises regarding humeral head and distal articulation proportions. Instead,
23 even though some ratios of the humeral head seem to present a strong phylogenetic
24 signal, our analyses favor the interpretation of a less specialized kind of

1 quadrupedalism. Proportions of the distal epiphyses overlap with many primate groups
2 including omomyids, as well as extant strepsirrhines and platyrrhines. This suggests that
3 telling apart distal humeral remains of strepsirrhines and haplorhines in early forms can
4 be problematic. It is possible that the humeral specializations lag behind other regions
5 of the skeleton during locomotor differentiation. If so, the slow-climbing hypothesis
6 could still potentially be correct. However, this would have to be tested by studies
7 comparing the behavioral signal in multiple elements for the same species.

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12

13 **Figure and table legends**

14 Figure 1. *Adapis* humeri attributed to morphotype 1. Complete specimen: ISE-M-ROS-
15 2-95; Proximal ends: ISE-M-ROS-2-536, Vi-Ros-563*; Distal ends: ISE-M-ROS-2-
16 534*, ISE-M-ROS-2-535*, QW 1481. For each bone, successive views are from left to
17 right anterior, posterior, lateral and medial; plus proximal view for proximal ends, disto-
18 anterior view for distal parts, and distal view when the distal part includes articular
19 surfaces. Specimens marked with an asterisk are reversed for comparison purposes.
20 Scale bar represents 1 cm.

1 Figure 2. *Adapis humeri* attributed to morphotype 2. Complete specimen: Ma-PhQ-332;
2 Proximal ends: ISE-M-ROS-2-80; Distal ends: ISE-M-ROS-2-79, Vi-Ros-640. Same
3 views as on Figure 1. Scale bar represents 1 cm.

4 Figure 3. *Adapis humeri* attributed to morphotype 3. Specimen missing humeral head:
5 MNHN-Qu-16583; Distal ends: FSM-PQ-1744, Vi-Esc-839*, ISE-M-ECA-1364*.
6 Specimens marked with an asterisk are reversed for comparison purposes. Same views
7 as on Figure 1. Scale bar represents 1 cm.

8 Figure 4. *Adapis humerus* attributed to morphotype 4. Single specimen missing
9 laterodistal end: MNHN-ACQ-262*. Same views as on Figure 1. The specimen is
10 marked with an asterisk because it is reversed for comparison purposes. Scale bar
11 represents 1 cm.

12 Figure 5. *Adapis humerus* attributed to morphotype 5. Single specimen missing humeral
13 head: AMNH-FM-10018. Same views as on Figure 1. Scale bar represents 1 cm.

14 Figure 6. *Adapis humeri* attributed to morphotype 6. Complete specimen: MNHN-Qu-
15 16584*; Specimens missing humeral head: Ma-PhQ-330; Specimens missing humeral
16 head and some parts of the distal articulation: Ma-PhQ-331*, Ma-PhQ-333. Specimens
17 marked with an asterisk are reversed for comparison purposes. Same views as on Figure
18 1. Scale bar represents 1 cm.

19 Figure 7. Anatomical terms used in the descriptions. 1: greater tuberosity; 2: lesser
20 tuberosity; 3: bicipital groove or intertubercular sulcus; 4: infraspinatus fossa; 5:
21 deltopectoral crest; 6: teres major tubercle; 7: brachioradialis flange; 8: capitulum;
22 9: trochlea; 10: entepicondylar foramen; 11: radial fossa; 12: olecranon fossa; 13: medial
23 epicondyle; 14: lateral epicondyle; 15: capitular tail; 16: zona conoidea (if present); 17:
24 articular surface of the humeral head; 18: deltoid V, channel of insertion of the deltoid

1 muscle on the humeral shaft; 19: coronoid fossa; 20: anterior epitrochlear fossa; 21:
2 posterior epitrochlear fossa. Humerus used is MNHN-Qu-16584, reversed. Scale bar
3 represents 1 cm.

4 Figure 8. Measurements taken on *Adapis* humeri as well as some other primates used
5 for comparisons. Total L: total length of the humerus; Total L w/o head: total length of
6 the humerus without the humeral head; Height derived from ML distal: height of the
7 humeral head derived from distal mediolateral width of the humeral head; PD central:
8 central proximodistal length of the humeral head; ML distal: distal mediolateral width
9 of the humeral head; TL: trochlear length; CL: capitulum length; TH: trochlear height;
10 EEC: entepicondylar width; TW: trochlear width; CW: capitulum width; AW: articular
11 width. Total L following Ford (1988); H derived from ML distal, PD central and ML
12 distal following Schmitt (1996); TL, CL, TH, TW, CW and AW following Szalay and
13 Dagosto (1980); EEC following Boyer et al. (2010). Humerus used is MNHN-Qu-
14 16584, reversed.

15 Figure 9. Plot of humeral head indices comparing fossil and extant taxa, following
16 Schmitt (1996). A) Distal mediolateral width (ML distal in Figure 8) divided by central
17 proximodistal length of the humeral head (PD central in Figure 8). 1: ISE-M-ROS-2-
18 536; 2: MNHN-ACQ-262; 3: ISE-M-ROS-2-95 and Ma-PhQ-332; 4: MNHN-Qu-
19 16584; 5: Vi-Ros-563; 6: ISE-M-ROS-2-80; B) Height of the humeral head derived
20 from the distal mediolateral width (Height derived from ML in Figure 8) divided by the
21 distal mediolateral width (ML distal in Figure 8). 7: ISE-M-ROS-2-80 and ISE-M-ROS-
22 2-95; 8: MNHN-ACQ-262; 9: Ma-PhQ-332; 10: Vi-Ros-563; 11: MNHN-Qu-16584;
23 12: ISE-M-ROS-2-536. Locomotor categories include: AQ (arboreal quadrupedalism),
24 QRC (quadrupedal runner and climber), VCL (vertical clinger and leaper), SC (slow

1 climber), MIXED (quadrupedal walker, leaper and runner with suspension in some
2 cases).

3 Figure 10. Principal components analysis results of four distal humeral measurements
4 following Boyer et al. (2010). Data taken from Szalay and Dagosto (1980), Senturia
5 (1995), Rose et al. (2009), Boyer et al. (2010), Dunn et al. (2016) and this paper. A,
6 PCA results obtained with several groups of living platyrrhines and catarrhines. B, PCA
7 results obtained after the removal of the living anthropoid groups.

8 Figure 11. Comparison of humeri of different extinct and extant primates. *Adapis* group
9 morphotypes used as example are morphotypes 2 (M2, Ma-PhQ-332) and 6 (M6,
10 MNHN-Qu-16584*) because they present the most complete specimens of the humeri
11 studied in this paper. *Leptadapis magnus* is represented in the figure by two different
12 specimens: QD 663 for anterior, posterior and distal views, and QD 664 for medial and
13 lateral views. Specimens marked with an asterisk are reversed for comparison purposes.
14 For more information on specimens used see Table 4. All scales represent 1 cm.

15 Table 1. Complete list of all *Adapis* group humeri included in this paper with
16 information on morphotype (MT) attribution, species attribution, preservation, locality
17 and institution. (R) right humerus; (L) left humerus; (AMNH) American Museum of
18 Natural History, New York, USA; (MNHN) Muséum National d'Histoire Naturelle,
19 Paris, France; (MHNVB) Muséum d'Histoire Naturelle Victor Brun, Montauban,
20 France; (NMB) Naturhistorisches Museum Basel, Basel, Switzerland. See Table 2 for
21 availability of specimens through online repositories MorphoSource and /or
22 MorphoMuseum.

1 Table 2. Humeri attributed to the *Adapis* group and used in this study with information
2 about the 3D surface reconstruction of each specimen and where to get it (online
3 repositories MorphoSource and /or MorphoMuseum), as well as citation instructions.

4 Table 3. Measurements and indices performed on *Adapis* specimens. Measurements
5 follow Ford (1988), Szalay and Dagosto (1980) and Schmitt (1996). Indices of the
6 proximal ends follow Schmitt (1996), and those of the distal ends follow Szalay and
7 Dagosto (1980).

8 Table 4. Comparative sample of humeri of different extinct and extant taxa. Institutional
9 abbreviations: AMNH (American Museum of Natural History, New York, NY, USA);
10 DLC (Duke Lemur Center, Durham, NC, USA); GU (Garhwal University, Srinagar,
11 Uttarakhand, India); MNHN (Museum National d'Histoire Naturelle, Paris, France);
12 NMB (Naturhistorisches Museum Basel, Basel, Switzerland); UM (University of
13 Michigan Museum of Paleontology, Ann Arbor, MI, USA); USNM (United States
14 National Museum, Smithsonian Institute, Washington, DC); VPL/JU/NKIM (Vertebrate
15 Palaeontology Laboratory, University of Jammu, Jammu, India). ¹ Doug M. Boyer,
16 Kenneth D. Rose and Rachel H. Dunn provided access to these data, originally
17 appearing in Dunn et al., 2016. The files were downloaded from
18 www.MorphoSource.org, Duke University. ² Gabriel S. Yapuncich provided access to
19 these data, the collection of which was funded by NSF BCS 1540421. ³ Measurements
20 taken directly on specimen at MNHN. ⁴ Doug M. Boyer provided access to these data
21 originally appearing in Boyer et al. (2013), the collection of which was funded by NSF
22 BCS 1440742 (to D.M. Boyer and G.F. Gunnell), NSF BCS 1440558 (to JI Bloch),
23 NSF BCS 1552848 (to D.M. Boyer). Permission to use media on MorphoSource
24 granted by copyright holder: AMNH. ⁵ Doug M. Boyer provided access to these data,
25 the collection of which was funded by NSF BCS 1440742 (to D.M. Boyer and G.F.

1 Gunnell), BCS 1440558 (to J.I. Bloch), NSF BCS 1558555, and NSF BCS 1552848.
2 Copyright Holder: USNM. All files with media number and/or doi number were
3 downloaded from www.MorphoSource.org, Duke University.

4 Table 5. Results of the statistical analyses of variance (Levene's test) performed using
5 measurements and indices of the distal articulation of humeral remains. Levene's test
6 compares variances of the *Adapis* group with similar-sized extant species (*Saimiri*
7 *sciureus*, *Haplemur griseus* and *Perodicticus potto*), as well as Vastan Mine primates:
8 the adapiform *Marcgodinotius indicus*, the omomyids *Vastanomys major* and *V.*
9 *gracilis*, and other unattributed euprimate remains from the same site. *Only significant
10 results are included in this table (p -values <0.05). A significant result indicates that more
11 morphological variation is present in the *Adapis* group than in the comparison group.

12 SOM 1. Summary of the main features presented by the different *Adapis* humeri studied
13 in this work.

14 SOM 2. Complete descriptions and comparisons of all the *Adapis* group humeri studied
15 in this paper arranged depending on morphotype attribution.

16 SOM 3. Comparative data on distal humeral indices. Data on trochlear articular index
17 [TAI=(TW/AW)*100] and trochlear height-width index [THWI=(TH/TW)*100] from
18 Szalay and Dagosto (1980) except for humeri described in this paper and Vastan Mine
19 specimens appearing in Dunn et al. (2016). Data on locomotion following Fleagle
20 (1988), Ankel-Simons (2007) and Gebo (2011).