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## RESEARCH ARTICLE

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# 3D geometric morphometrics analysis of mandibular fragments of *Ouranopithecus macedoniensis* from the late Miocene deposits of Central Macedonia, Greece

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## Abstract

**Objectives:** To explore mandibular shape differences between *Ouranopithecus macedoniensis* and a comparative sample of extant great apes using three-dimensional (3D) geometric morphometrics. Other objectives are to assess mandibular shape variation and homogeneity within *Ouranopithecus*, explore the effects of size on mandibular shape, and explore the degree of mandibular sexual size dimorphism in *Ouranopithecus*.

**Materials and methods:** The comparative sample comprises digitized mandibles from adult extant great apes. The 3D analysis includes three datasets: one with landmarks registered on the mandibular corpus and symphysis of mandibles preserving both sides, one on hemimandibles only, and one focused on the ramus and gonial area. Multivariate statistical analyses were conducted, such as ordination analyses (PCA), intra-specific Procrustes distances pairs, pairwise male–female centroid size differences, and correlation analyses.

**Results:** The male and female specimens of *Ouranopithecus* have mandibular shapes that are quite similar, although differences exist. The Procrustes distances results suggest more shape variation in *Ouranopithecus* than in the extant great apes. *Ouranopithecus* shows some similarities in mandibular shape to the larger great apes, *Gorilla* and *Pongo*. Moreover, the degree of sexual dimorphism in the small *Ouranopithecus* sample is greater than any of the great apes. Based on our correlation analyses of principal components (PC) with size, some PCs are significantly correlated with size, with correlation varying from moderate to substantial.

**Discussion:** This study attempted to understand better the variation within the mandibles of *O. macedoniensis* and the expression of sexual dimorphism in this taxon in more detail than has been done previously. The overall mandibular morphology of *Ouranopithecus* shows some similarities to those of the larger great apes, which likely reflects similarities in size. Compared to *Gorilla* and *Pongo*, *O. macedoniensis* shows an elevated degree of morphological variation, although limitations relating to sample size apply. Sexual dimorphism in the mandibles of *O. macedoniensis* appears to be relatively high, seemingly greater than in *Gorilla* and high even in comparison to *Pongo*, but this again is possibly in part an artifact of a small sample size.

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## KEYWORDS

hominoid evolution, mandibular variation, Miocene hominoids, sexual dimorphism, virtual anthropology

## 1 | INTRODUCTION

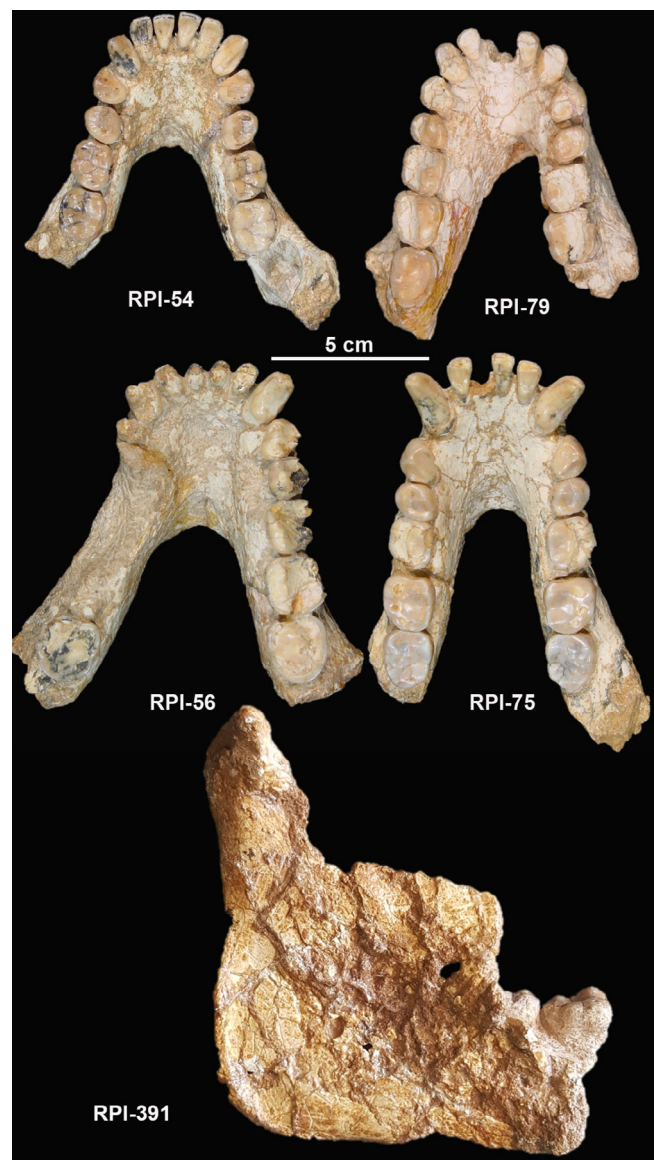
Ravin de la Pluie (RPI) in the Axios valley is one of the three localities where the material of *Ouranopithecus macedoniensis* has been found to date. The rich material from RPI includes maxillary and mandibular remains numerous isolated teeth, and a few post-cranial specimens (de Bonis, 1974; de Bonis et al., 1990, 1998; de Bonis & Koufos, 2014; de Bonis & Melentis, 1977, 1978; Koufos & de Bonis, 2006; Koufos, de Bonis, & Kugiumtzis, 2016). De Bonis and Koufos (1994) interpreted the material from RPI as consisting of individuals that most probably died at the same time during a single river flood event based on the geology of this locality. Additionally, ongoing excavations in the other two *O. macedoniensis* localities, Xirochori 1 (XIR), in the Axios valley, and Nikiti 1 (NKT), in the Chalkidiki Peninsula, have produced other very important specimens, including an almost complete face (XIR-1; de Bonis et al., 1990; Koufos, 1993, 1995). Based on faunal correlation and magnetostratigraphic evidence at these three localities, the chronostratigraphic range of *O. macedoniensis* is between 9.6 and 8.7 Ma (Koufos, Kostopoulos, & Vlachou, 2016; Sen et al., 2000).

While there are several well-preserved *O. macedoniensis* mandibles, only a few studies have been conducted on these (de Bonis & Koufos, 1993, 1994; de Bonis & Melentis, 1977; Koufos, 1993). None of the previous work assessed the mandibular shape of *O. macedoniensis* using more advanced techniques, such as geometric morphometrics (GM). GM is a quantitative means of analyzing shape (Corti, 1993; Slice, 2007), and allows for more informative documentation of shape differences than traditional morphometric techniques (Adams et al., 2004; Slice, 2007).

Here we investigate the mandibular specimens from RPI, including four partial mandibles preserving both corpora and the symphysis (RPI-54, RPI-56, RPI-75, and RPI-79) and RPI-391, a right mandibular ramus (Figure 1). Most of the specimens have well-preserved dentitions, and apart from one specimen, their overall shape appears undistorted, presenting only minor taphonomic damage. With this study, we aim to explore mandibular shape variation between *Ouranopithecus* and a comparative sample of extant great apes (*Gorilla*, *Pan*, and *Pongo*), using three-dimensional (3D) geometric morphometrics. We also assess patterns of variation within *Ouranopithecus*, especially as they relate to sexual dimorphism compared to those of the extant great apes. Lastly, we address the effects of size-related shape differences among taxa. Questions to be discussed in this study include, (a) Does mandibular shape vary between males and females of *Ouranopithecus macedoniensis*? (b) Is the mandibular shape of *Ouranopithecus macedoniensis* distinct from those of the extant great apes? (c) How do size and sexual dimorphism in *Ouranopithecus macedoniensis* compare to those of extant great apes?

1.1 | Mandibular morphology and sexually dimorphic traits in *Ouranopithecus macedoniensis*

The mandibular shape of *Ouranopithecus* has been described previously (de Bonis & Koufos, 1993, 1994; de Bonis & Melentis, 1977; Koufos, 1993) as preserving a primitive symphysis with well-marked superior and inferior tori and having powerful chewing capacity, based on the morphology of the gonial area and the well-marked crest



**FIGURE 1** The four *O. macedoniensis* partial mandibles (RPI-54, RPI-79, RPI-75, and RPI-56) and the RPI-391 ramus. Photographs by G. D. Koufos and M. Ioannidou

(masseteric tuberosity) (de Bonis & Koufos, 2001). It also retains an antero-posteriorly narrow mandibular condyle, a trait that differentiates it from the extant great apes, in which the condyle is more robust. Although *O. macedoniensis* is recognized as a single-species, it is characterized by strong dental sexual dimorphism in the post-canine dentition, which is greater than that of the larger great apes, *Gorilla* and *Pongo* (Koufos, de Bonis, & Kugiumtzis, 2016; Schrein, 2006; Scott et al., 2009). Traits likely related to sexual dimorphism can also be observed in the mandible of *Ouranopithecus*, with male mandibles being larger and more robust than those of the females (de Bonis & Melentis, 1977; Koufos, 1993). However, dental dimorphism, particularly the morphology and size of the canines and the size of the post-canine lower teeth, is more commonly studied because of the abundance of teeth in fossil assemblages. Here, we address this imbalance by examining the expression of sexual dimorphism in the mandibles of *Ouranopithecus* in more detail than has been done previously.

## 2 | MATERIALS AND METHODS

### 2.1 | Sample

#### 2.1.1 | *Ouranopithecus macedoniensis* specimens

All the RPI material was micro-CT scanned at the Paleoanthropology High Resolution Computed Tomography Laboratory, University of Tübingen (Phoenix X-Ray, v/tomex/s GE, tube voltage 220 kV, tube current 210 mA, and 0.6 mm copper filter).

**RPI-54:** This mandible, the type specimen of *O. macedoniensis* (first attributed to *Dryopithecus macedoniensis*; de Bonis, 1974), belongs to a late juvenile/young adult individual, and it is a female based on the size and shape of its canine (de Bonis, 1974; Kelley, 1995). It preserves the entire dentition except the left M<sub>3</sub>; the right M<sub>3</sub> is not yet erupted. The teeth are well preserved and hardly worn. Additionally, the mandible preserves both corpora and the symphysis, while both ascending rami are missing (de Bonis, 1974; de Bonis & Melentis, 1977; Figure 1).

**RPI-56:** This specimen belongs to an old male individual, based on canine size and dental wear (de Bonis & Melentis, 1977). It does not preserve its entire dentition, but many teeth are present (I<sub>1</sub> to M<sub>3</sub> right; I<sub>1</sub> to P<sub>3</sub>, and M<sub>3</sub> left). Both corpora and symphysis are well preserved, and both ascending rami are missing (de Bonis, 1974; de Bonis & Melentis, 1977; Figure 1).

**RPI-75:** This specimen preserves the entire permanent dentition. Canine size and shape indicate that it belongs to a male individual (Kelley, 1995). Both corpora of the mandible are well preserved, although both are partly damaged on the lateral surface at the level of the P<sub>4</sub> due to post-mortem taphonomic processes. However, the overall shape is unaltered. Both ascending rami are missing (de Bonis & Melentis, 1977; Figure 1).

**RPI-79:** This mandible belongs to a female individual, based on its canine size. It has an almost complete permanent dentition, as only the right M<sub>3</sub> is missing. The teeth are quite worn. Both corpora and

symphysis of this mandible are present; however, the right corpus and symphysis exhibit displacement from the midplane due to post-mortem taphonomic processes. Both ascending rami are missing (Figure 1).

**RPI-391:** This specimen probably belongs to a male individual, determined from the large size of the teeth preserved, while based on the dental wear, it is younger than RPI-75 (de Bonis & Koufos, 1993). The right ramus and part of the corpus are preserved, with M<sub>2</sub> and M<sub>3</sub> present (Figure 1). The coronoid process is partly preserved, although its superior part is missing along with the sigmoid notch. While the overall shape appears largely undeformed, a slight flattening can be observed. Moreover, the condyle is fairly complete, preserving the glenoid process and glenoid fossa, although the area below the condyle is broken and distorted, without altering its shape (de Bonis & Koufos, 1993, Figure 1).

#### 2.1.2 | Comparative sample

Fifty-three mandibles from adult extant great apes were digitized, including *Gorilla gorilla gorilla* ( $n = 17$ ), *Pan troglodytes* ( $n = 19$ ), and *Pongo pygmaeus pygmaeus* ( $n = 17$ ) (Table 1). Variation in the *P. troglodytes* sample may exist, as the subspecies composition is unknown (see Taylor & Groves, 2003; Robinson, 2012 for variation in *Pan* subspecies). All extant taxa are represented by both adult female and male individuals. Adult status was established using the criterion of full eruption of the permanent third molar. The landmarks were registered on 3D models of mandibles obtained from either medical CT scans or surface scans using the EVA Artec (Artec Group, Luxembourg, Luxembourg) handheld high precision scanner, property of the Paleoanthropology High Resolution Computed Tomography Laboratory, University of Tübingen.

## 2.2 | Landmarks and error test

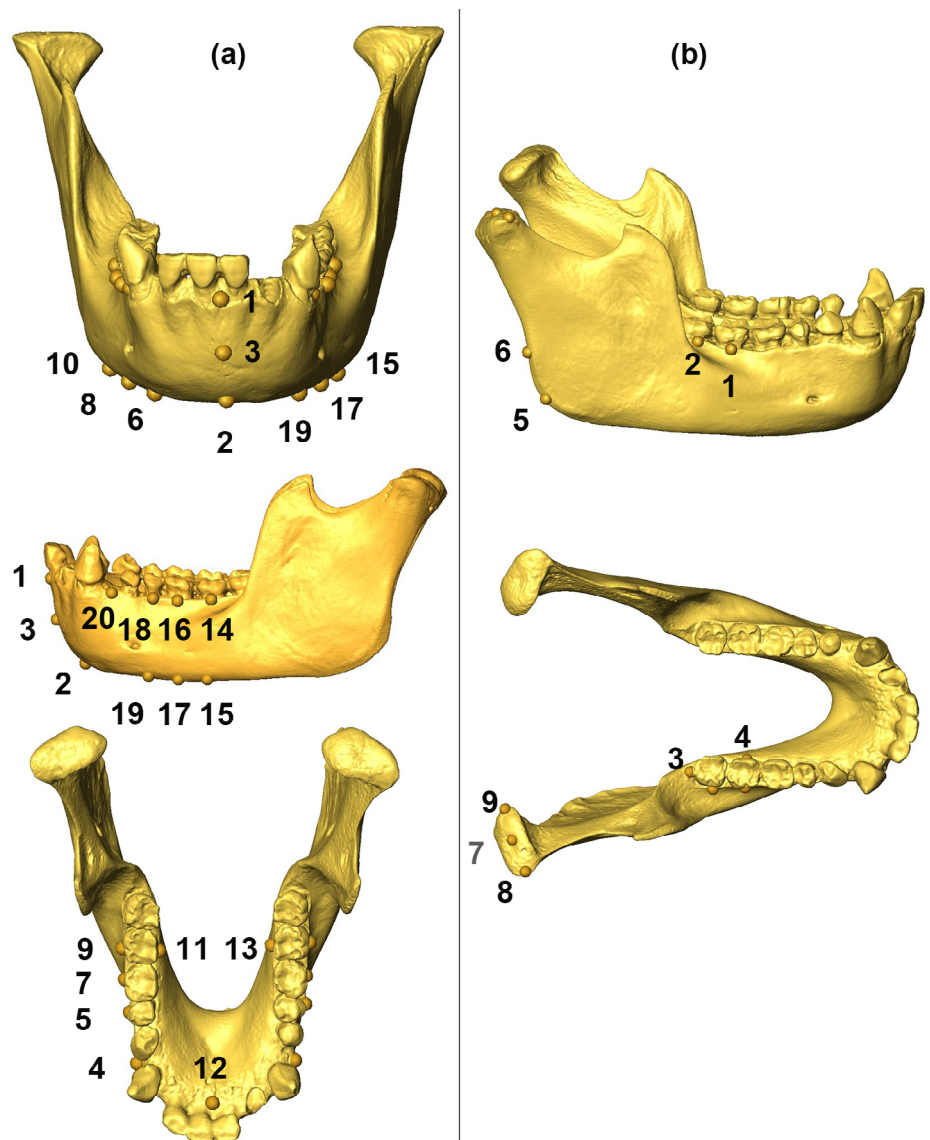
The analysis included three datasets: one with bilateral landmarks on both mandibular corpora and symphysis (20 landmarks; Figure 2a; Table 2); one with landmarks registered on the hemimandible (left side

**TABLE 1** Number of extant great ape and *Ouranopithecus macedoniensis* specimens used in this study

Species	Sex		Collection <sup>a</sup>
	Male	Female	
<i>Gorilla gorilla</i>	8	9	1,2
<i>Pan troglodytes</i>	10	9	1,3,4
<i>Pongo pygmaeus</i>	9	8	2,3,4
<i>Ouranopithecus macedoniensis</i>	2	2	5

<sup>a</sup>1: Natural History Museum, Stuttgart; 2: Smithsonian National Museum of Natural History; 3: Natural History Museum, Berlin; 4: Senckenberg Museum of Natural History, Frankfurt; 5: Aristotle University, Thessaloniki.

**FIGURE 2** Three-dimensional (3D) landmarks used in the analyses, registered on a surface scan of a female *Pan troglodytes* mandible. (a) Corpus and symphysis (for the hemimandible analysis landmarks 1–3 and 12–20 were used); (b) ramus



including corpus and symphysis; 12 landmarks); and one on the ramus and gonial area (right side; 9 landmarks in total; Figure 2b; Table 2). The registration of the landmarks was carried out in Avizo software (©FEI Visualization Sciences Group, version 9.1). The landmarks were collected along both corpora (bilateral analysis), symphysis, and ramus of the mandible to analyze variation in height, length, and width in the anatomical areas selected. In the first dataset, the missing landmarks of the mandible RPI-56 (landmarks 13, 14, 16, and 18) were reconstructed using reflected relabeling of the existing landmarks of the right side (Gunz et al., 2009). The second dataset was used to include RPI-79, which was excluded from the bilateral analyses because the right side shows displacement from the mid-sagittal plane (landmarks 1–3 and 12–20 were used; Table 2). The landmarks selected for this study are a combination of landmarks (Type I, II, and III) used in previous studies by Nicholson and Harvati (2006), Miller et al. (2008), Zollikofer et al. (2009), Robinson (2012); and Singh (2014). Type I landmarks correspond to standard identifiable osteometric points, as opposed to type II and III, which mostly

characterize an anatomical region (Bookstein, 1991). Most of the landmarks used in this study are Type II and III since Type I landmarks are not easily definable on the mandible. All landmarks were collected by MI. Intra-observer error was evaluated based on a standard deviation threshold of 5% (Robinson & Terhune, 2017) and assessed by collecting the landmarks from the same specimen five times over a period of 2 weeks. The precision of the landmark registration was considered acceptable, as the standard deviation of each landmark was significantly lower than the threshold, ranging from 0.38% to 1.05% (see Table 2).

### 2.3 | Statistical analyses

The landmark configurations from all three datasets were subjected to generalized Procrustes analysis (GPA) in EVAN Toolbox (Version 1.6; EVAN-Society, e.V.), which superimposes (scales, translates, and rotates) all the landmark configurations and produces the

**TABLE 2** List of landmarks, definitions, and intra-observer error for bilateral and ramus analyses. For the hemimandible analysis the landmarks used are: 1–3 and 12–20

Count	Landmarks	Definition	Error (%)
<i>Bilateral analysis</i>			
1	Infradentale (id)	Midline point at the superior tip of the alveolar border between the mandibular central incisors <sup>a</sup>	0.38
2	Gnathion (gn)	Most anterior midline point on the chin of the mandible <sup>a</sup>	0.65
3	Mid-point between landmarks 1 (id) and 2 (gn)	Point in-between landmarks 1 (id) and 2 (gn)	0.96
4, 20	C–P <sub>3</sub> alveolar R/L	Point on alveolar border between C and P <sub>3</sub>	0.72/0.80
5, 18	P <sub>4</sub> superior R/L	Midline point of the P <sub>4</sub> alveolus	0.62/0.65
6, 19	P <sub>4</sub> inferior R/L	Point on the bottom of the mandibular corpus below P <sub>4</sub>	1.05/0.77
7, 16	M <sub>1</sub> superior R/L	Midline point of the M <sub>1</sub> alveolus	0.52/0.70
8, 17	M <sub>1</sub> inferior R/L	Point on the bottom of the mandibular corpus below M <sub>1</sub>	0.88/0.90
9, 14	M <sub>2</sub> superior R/L	Midline point the middle of the M <sub>2</sub> alveolus	0.59/0.61
10, 15	M <sub>2</sub> inferior R/L	Point on the bottom of the mandibular corpus below M <sub>2</sub>	0.98/1.02
11, 13	Endomolare R/L	Most medial point on the inner surface of the alveolar margin opposite the center of the M <sub>2</sub> crown <sup>a</sup>	1.04/0.90
12	Mandibular orale	Most superior tip at the lingual side of the alveolar border between central incisors	0.70
<i>Ramus</i>			
1	Right M <sub>2</sub> superior	Point at the middle of the M <sub>2</sub> alveolus	0.74
2	Right M <sub>3</sub> superior	Point at the middle of the M <sub>3</sub> alveolus	0.70
3	Right midpoint distal M <sub>3</sub> alveolar border	Midpoint on the distal surface of the alveolar margin of the M <sub>3</sub>	0.48
4	Right endomolare	Most medial point on the inner surface of the alveolar margin opposite the center of the M <sub>2</sub> crown <sup>a</sup>	0.88
5	Right gonion (g)	Most lateral, posterior, and inferior point at the vertex of the curve of the mandibular angle	0.79
6	Right posterior ramus	Point at the posterior margin of ramus at level of M <sub>3</sub>	0.93
7	Right condyle superior	Most superior point on the mandibular condyle	0.50
8	Right condyle lateral	Most lateral point on the mandibular condyle	0.74
9	Right condyle medial	Most medial point on the mandibular condyle	0.62

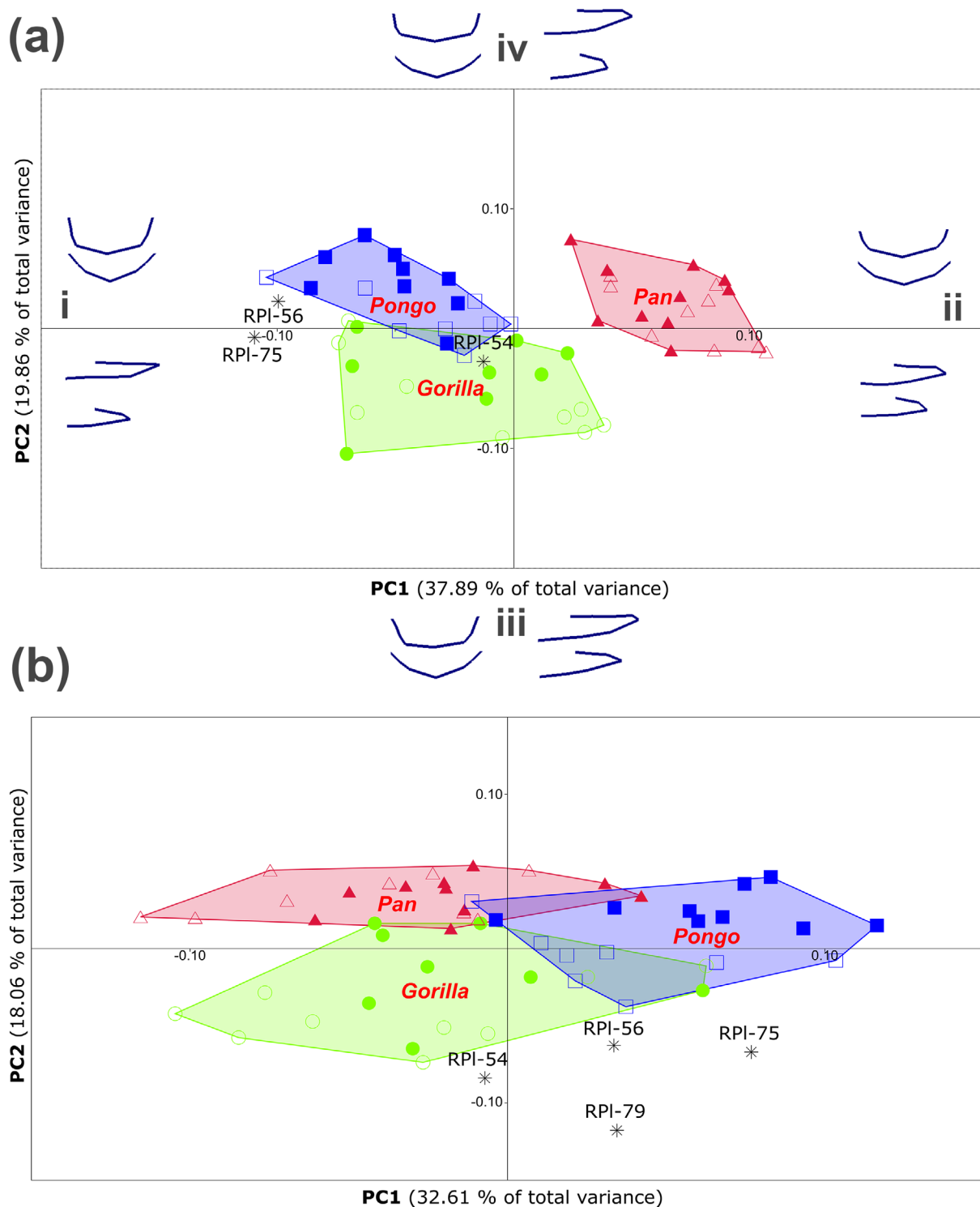
<sup>a</sup>As defined in White et al. (2011).

superimposed Procrustes shape coordinates (Bookstein, 1997; Rohlf, 1993; Slice, 2007). A principal component analysis (PCA) was conducted on all the datasets in shape space, using PAST (Version 4.05; Hammer et al., 2001). The PCA in shape space was performed on the Procrustes shape coordinates in order to examine the overall mandibular shape variation of all specimens. We also conducted permutation tests between sexes of each extant species (separately) to test if there are sex differences in each species, using R (Geomorph package; Adams & Otárola-Castillo, 2013; 1000 permutations). While Procrustes superimposition eliminates size as a variable, it does not eliminate allometric size-related effects. We, therefore, conducted a correlation analysis between the first two principal components and log centroid size (on all datasets), using Pearson's correlation coefficient, to investigate whether the distribution of the specimens in the

PCA is influenced by size. In addition, we used Procrustes distances to explore shape difference within the *Ouranopithecus* sample compared to that present in each of the extant species. Using boxplots, we compared all pairwise distances in *Ouranopithecus* with those of each extant ape. The differences in the means of inter-individual distances among *Ouranopithecus* and the extant great apes were tested for significance (one-way ANOVA in SPSS; IBM® SPSS® Statistics 27). We also calculated the 95% probability intervals from all pairwise Procrustes distances for each great ape species and located the pairwise distances for *Ouranopithecus* with respect to these. These analyses were performed in order to investigate whether there is more variation in the small *Ouranopithecus* sample than in the extant great apes. To investigate the degree of sexual dimorphism expressed by the *Ouranopithecus* mandibles and to compare it to levels of sexual

dimorphism in the extant great apes, we plotted the pairwise *Ouranopithecus* male–female centroid size differences within a distribution of all male–female pairwise differences for each extant great ape, using boxplots. We also calculated the differences between the male and

female centroid means, which were also tested for significance (only great apes; independent-samples *t*-test were run in SPSS). As the sample size of *Ouranopithecus* is so small (and there is only one female specimen in the bilateral analysis), the significance test could not be performed.



**FIGURE 3** PCA results of the bilateral (a) and hemimandible (b) analyses in shape space: (a) PC1 (37.89%) vs PC2 (19.86%). (i–iv) Shape changes, in frontal and lateral view, for negative and positive extreme values associated with PC1 (i and ii) and PC2 (iii and iv); and (b) PC1 (32.61%) versus PC2 (18.06%). Convex hulls for *Gorilla*—green circle; male (filled symbol), female (open symbol), *Pan*—red triangle; male (filled symbol), female (open symbol) and *Pongo*—blue square; male (filled symbol), female (open symbol)

### 3 | RESULTS

#### 3.1 | Principal component analysis

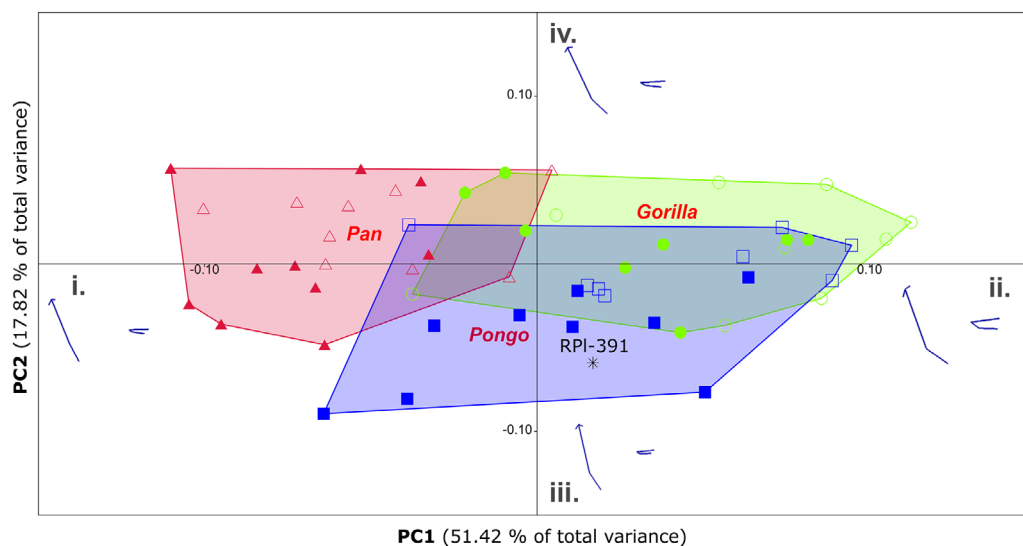
Bilateral analysis: Figure 3a displays the first two principal components (PCs), which together account for 57.75% of total shape variation. PC1 is associated with changes in the length of the mandible and width of the dental arcade, and PC2 with symphysis height. The scores along these first two PCs show a clear separation among all three extant taxa, although there is some overlap between the convex hulls of *Gorilla* and *Pongo*. The permutation tests show significant male–female differences along the PC axes in *Pongo* (Goodall's *F* statistics = 2.94,  $p < 0.01$ ), but not in *Gorilla* and *Pan* (Goodall's *F* statistics = 1.19,  $p = 0.29$ ; Goodall's *F* statistics = 1.83,  $p = 0.06$ ; respectively). The male *Ouranopithecus* specimens (RPI-75 and RPI-56) plot close together, outside of any convex hull and on the negative end of PC1, while the single female (RPI-54) plots within the *Gorilla* convex hull. Low PC1 scores (37.89% of total shape variation) indicate a relatively antero-posteriorly elongate mandible and medio-laterally narrow dental arcade relative to mandibular length, while high scores indicate a relatively antero-posteriorly shorter mandible and medio-laterally wider dental arcade (Figure 3a, i and ii, respectively). Low PC2 scores (19.86% of total shape variation) indicate a relatively supero-inferiorly shallow corpus and symphysis, while high scores reflect a relatively supero-inferiorly deeper corpus and symphysis (Figure 3a, iii and iv, respectively). When the first two PCs were tested for correlation against long centroid size, PC1 was significantly correlated with centroid size ( $r = -0.67$ ,  $p < 0.01$ ), while PC2 was not ( $r = -0.08$ ,  $p = 0.51$ ).

The male mandibles of *Ouranopithecus* are antero-posteriorly elongate with a relatively medio-laterally narrow dental arcade, while the female mandibular shape is antero-posteriorly shorter and has a relatively medio-laterally wider dental arcade. The mandibles of

*Ouranopithecus* also have relatively supero-inferiorly deeper corpus and symphysis than many individuals of *Gorilla*, but relatively shallower than many *Pan* and *Pongo* individuals. However, overall the shape is more similar to the mandibular shape of the larger great apes, *Pongo* and *Gorilla*, than *Pan*.

Hemimandible: The first two PCs account for 50.67% of total shape variance (Figure 3b). Although there is partial overlap among the convex hulls of the extant taxa, the three great ape genera are relatively distinct along these axes. The permutation tests show no significant male–female difference in *Gorilla* (Goodall's *F* statistics = 1.56,  $p = 0.12$ ), while this difference is significant in *Pan* and *Pongo* (Goodall's *F* statistics = 2.48,  $p < 0.01$ ; Goodall's *F* statistics = 2.23,  $p < 0.01$ ; respectively). Three of *Ouranopithecus* specimens cluster on the positive end of PC1, with RPI-54 being slightly negative, outside the convex hulls of the extant taxa but closer to those of *Gorilla* and *Pongo*. RPI-75 plots relatively distant from the other male (RPI-56), and two female specimens. As for size-PC correlations, PC1 is moderately but significantly correlated with centroid size ( $r = -0.43$ ,  $p < 0.01$ ), while PC2 is not ( $r = -0.15$ ,  $p = 0.26$ ). High PC1 scores (32.61% of total shape variation) indicate a relatively antero-posteriorly elongate hemimandible, while low scores indicate a relatively antero-posteriorly shorter hemimandible. Low PC2 scores (18.06% of total shape variation) indicate a relatively supero-inferiorly shallow corpus, while high scores reflect a relatively supero-inferiorly deeper corpus.

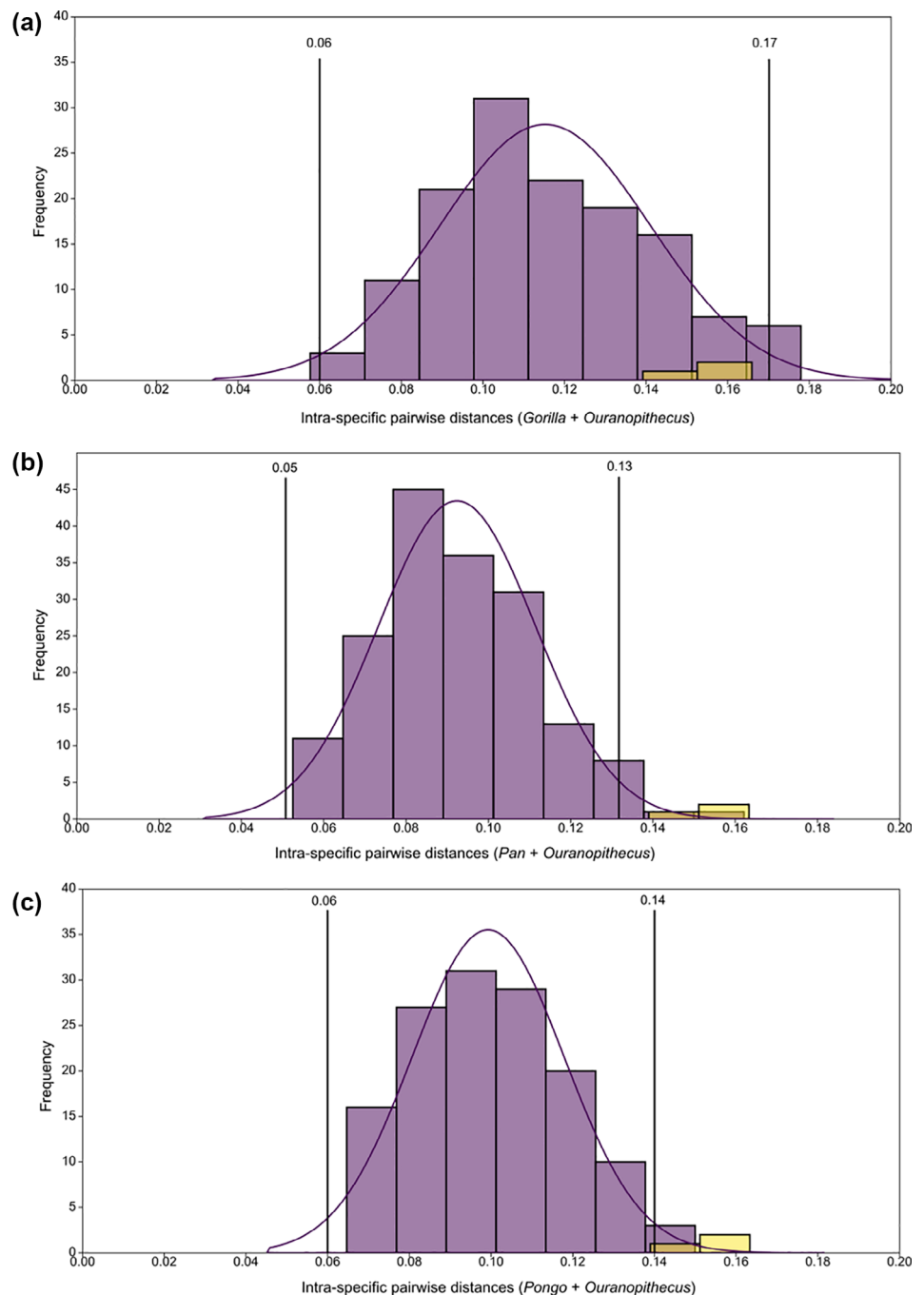
Ramus: Figure 4 displays the first two PCs, which together account for 69.24% of total shape variation. The convex hulls of the three extant taxa all overlap somewhat along these two axes. The permutation tests show no significant difference between females and males along the PC axes in *Gorilla* and *Pan* (Goodall's *F* statistics = 2.01,  $p = 0.08$ ; Goodall's *F* statistics = 1.95,  $p = 0.09$ ; respectively); while differences are significant in *Pongo* (Goodall's *F* statistics = 4.46,  $p < 0.01$ ). RPI-391 plots within the *Pongo* convex hull. High PC1 scores (51.42% of total variance)



**FIGURE 4** PCA results of the ramus dataset in shape space: PC1 (51.42%) vs PC2 (17.82%). (i–iv) Shape changes, in lateral view, for negative and positive extreme values associated with PC1 (i and ii) and PC2 (iii and iv)



**FIGURE 5** Distribution and density curve of pairwise intra-specific distances within species in extant great apes and *Ouranopithecus* (bilateral analysis). (a) *Gorilla* and *Ouranopithecus*, (b) *Pan* and *Ouranopithecus*, and (c) *Pongo* and *Ouranopithecus*



indicate a relatively more inferiorly and laterally positioned gonion with respect to the corpus, whereas low scores indicate a relatively more superiorly and medially positioned gonion. High PC2 scores (17.82% of total variance) indicate a relatively more wide gonial angle, while low PC2 scores indicate a relatively narrow angle. In this dataset, PC1 was significantly but mildly correlated with centroid size ( $r = 0.39$ ,  $p < 0.01$ ), while PC2 was not ( $r = -0.24$ ,  $p = 0.08$ ).

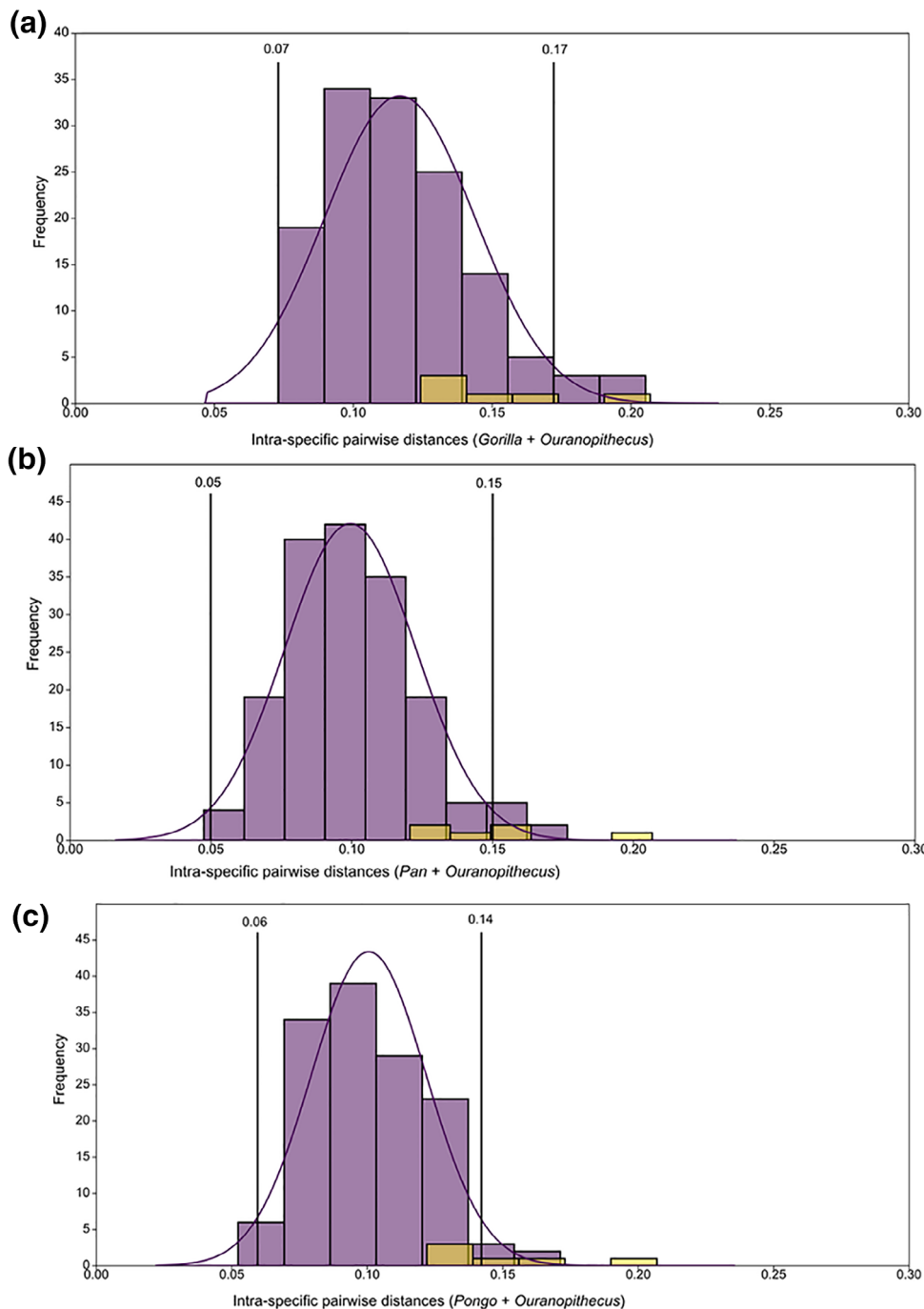
The ramus shape of *Ouranopithecus*, as it is represented by RPI-391, exhibits a relatively narrow gonial angle, similar to that of *Pongo* specimens.

### 3.2 | Procrustes distances

**Bilateral analysis:** The distances between the three *Ouranopithecus* specimens were either at the upper end or just outside the maximum range of the intra-specific distances of the extant species (Figure S1). The distances between the three *Ouranopithecus* mandibles fell within the 95% probability interval of the observed distribution of intra-specific pairwise distances of *Gorilla*, while they fell outside in the respective 95% probability intervals of *Pan* and *Pongo* (Figure 5). Moreover, there are significant differences in the means of the inter-individual distances between *Ouranopithecus* and *Pan* and *Pongo*,

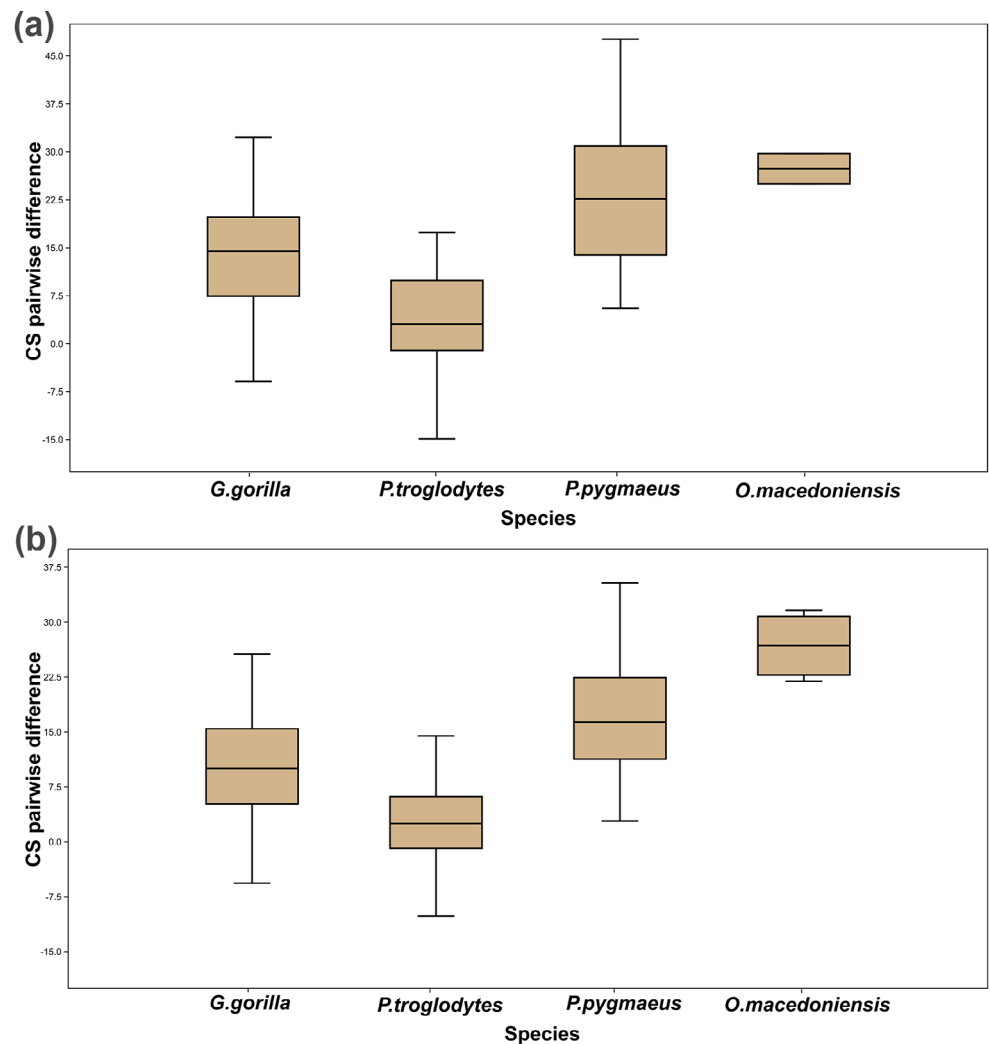
Species	<i>O. macedoniensis</i>	<i>G. gorilla</i>	<i>P. troglodytes</i>	<i>P. pygmaeus</i>
Bilateral analysis				
<i>O. macedoniensis</i>	—	ns	$p < 0.01$	$p < 0.01$
<i>G. gorilla</i>		—	$p < 0.01$	$p < 0.01$
<i>P. troglodytes</i>		$p < 0.01$	—	ns
<i>P. pygmaeus</i>		$p < 0.01$		—
Hemimandible				
<i>O. macedoniensis</i>	—	ns	$p < 0.01$	$p < 0.01$
<i>G. gorilla</i>		—	$p < 0.01$	$p < 0.01$
<i>P. troglodytes</i>		$p < 0.01$	—	ns
<i>P. pygmaeus</i>		$p < 0.01$		—

**TABLE 3** Inter-individual variability among *Ouranopithecus* and the extant great apes (one-way ANOVA)



**FIGURE 6** Distribution and density curve of pairwise intra-specific distances within species in extant great apes and *Ouranopithecus* (hemimandible analysis). (a) *Gorilla* and *Ouranopithecus*, (b) *Pan* and *Ouranopithecus*, and (c) *Pongo* and *Ouranopithecus*

**FIGURE 7** Boxplots of the pairwise male–female centroid size differences of *Ouranopithecus macedoniensis* and each of the extant great apes, (a) bilateral and (b) hemimandible analyses



**TABLE 4** Mean centroid sizes and results of independent-samples t-tests of males and females of the extant great apes and *O. macedoniensis*

	Male (mean)	Female (mean)	Male–female difference	T/p-value
Bilateral analysis				
<i>O. macedoniensis</i>	158.90	131.52	27.38	—
<i>G. gorilla</i>	169.13	153.88	15.26	−4.55/<0.01
<i>P. troglodytes</i>	138.14	132.33	5.81	−1.71/ns
<i>P. pygmaeus</i>	169.69	146.01	23.68	−6.8/<0.01
Hemimandible				
<i>O. macedoniensis</i>	110.79	84.01	26.78	—
<i>G. gorilla</i>	114.35	103.97	10.38	−3.97/<0.01
<i>P. troglodytes</i>	90.22	86.64	3.58	−1.72/ns
<i>P. pygmaeus</i>	116.27	99.93	16.34	−6.46/<0.01

while they are not significant between *Ouranopithecus* and *Gorilla* (Table 3).

**Hemimandible:** Similar to the bilateral analysis, the Procrustes distances between the four *Ouranopithecus* specimens were at the upper end of the intra-specific distances of the extant species (Figure S1). The pairwise distances between the *Ouranopithecus* hemimandibles fell within the 95% probability interval of *Gorilla*

(Figure 6), except for the distance between RPI-79 and RPI-56. Three of the *Ouranopithecus* pairwise distances (RPI-79 and RPI-56; RPI-79 and RPI-75; RPI-56 and RPI-75) fell outside the 95% probability intervals of *Pan* and *Pongo* (Figure 6). Differences in the means of the inter-individual distances between *Ouranopithecus* and *Pan* and *Pongo* are significant, while they are not significant between *Ouranopithecus* and *Gorilla* (Table 3).

Ramus: As there is only one specimen belonging to *Ouranopithecus macedoniensis*, we could only check to which individual the RPI-391 showed the closest Procrustes distance: it is most similar in its overall shape to a male *Pongo* individual (Table S1).

### 3.3 | Sexual dimorphism

Bilateral analysis: Figure 7a contains boxplots showing the pairwise male–female centroid size differences in the extant great apes and *Ouranopithecus*. The largest differences are in *Pongo*, while the smallest are in *Pan*. The *Ouranopithecus* male–female differences fall in the range of *Pongo* male–female pairs but also the upper part of the *Gorilla* range. *Ouranopithecus* shows the greatest mean differences in male–female pairwise comparisons (Table 4; see also Table S2). Significance tests on male–female centroid means of each great ape species indicated a significant difference between the means of the sexes in *Gorilla* and *Pongo*, but not in *Pan* (Table 4; see also Figure S2). Figure S2 illustrates the male–female centroid size differences in *Gorilla*, *Pongo*, *Pan*, and *Ouranopithecus*. The centroid size differences in *Ouranopithecus* show a significant difference between the two males and one female, as in *Gorilla* and *Pongo*.

Hemimandible: *Ouranopithecus* again exhibits the greatest pairwise differences between males and females in this dataset. Among the extant great apes, the greatest differences are in *Pongo*, while the lowest are in *Pan* (Table 4; Figure 7b; see also Table S2). Significance tests on male–female centroid means of each great ape species indicated a significant difference among species in *Gorilla* and *Pongo*, but not in *Pan* (Table 4; see also Figure S3). The centroid size differences in *Ouranopithecus* show that there is a significant difference between males and females, as in *Gorilla* and *Pongo* (Figure S3).

## 4 | DISCUSSION

Variation in mandibular shape in primates reflects a combination of complex factors, such as adaptive response to biomechanical loads and feeding behavior (e.g., Beecher, 1977; Daegling & Jungers, 2000; Taylor, 2002; Terhune, 2013), sexual dimorphism (e.g., Collard & Wood, 2001; Humphrey et al., 1999; Robinson, 2003) or taxonomy (e.g., Daegling & Jungers, 2000; Kelly & Pilbeam, 1986). With respect to the great apes, differences in mandibular shape exist to some extent at the genus level across great apes, in the corpus and symphysis (e.g., Daegling & Jungers, 2000; Guy et al., 2008; Pitirri & Begun, 2019), and ramus (e.g., Aitchison, 1965; Humphrey et al., 1999; Terhune et al., 2014). In general, the mandibles of the larger great apes, *Gorilla* and *Pongo*, are more similar to each other than they are to *Pan* (Collard & Wood, 2001; Humphrey et al., 1999; Robinson, 2003). Based on this knowledge, researchers have previously used the extant great apes as models to interpret mandibular variation and potential impact on taxonomic interpretations in fossil samples (e.g., Lague et al., 2008; Ritzman et al., 2016; Rosas & Bastir, 2004; Scott et al., 2009; Scott & Lockwood, 2004). Here, we

aimed to explore mandibular shape and size variation within *O. macedoniensis* in comparison to extant great apes in an attempt to understand better the variation within *O. macedoniensis* and the expression of sexual dimorphism in this taxon.

### 4.1 | Mandibular shape and homogeneity in *Ouranopithecus macedoniensis*

Our PCA results indicate that mandibular morphology, as represented by our 3D landmarks, can distinguish among extant great apes (even though some overlap exists) and *Ouranopithecus macedoniensis*. The *O. macedoniensis* mandibles are more similar in shape to the larger great apes, *Gorilla* and *Pongo*, than they are to *Pan*. Mandibular shape varies between males and females, as does size. The mandibular shape of male *Ouranopithecus*, in particular, is relatively long with a narrow dental arcade. The female *Ouranopithecus* mandible (RPI-54) is smaller but mainly exhibits broadly similar features as those of the male individuals, although shorter in length and height, and with a wider dental arcade in comparison to males. Overall, the *Ouranopithecus* mandibles appear to follow the pattern of similarity among the larger-bodied taxa observed previously (Collard & Wood, 2001; Humphrey et al., 1999; Robinson, 2003), with mandibles of *Gorilla* and *Pongo* be more similar to each other than they are to *Pan*.

The *O. macedoniensis* male mandibles cluster relatively close to each other in the PCA plots (bilateral and hemimandible analysis; Figure 3a–b). The female specimen (RPI-79), the only adult female examined here, also plots close to the male *Ouranopithecus* specimens in the hemimandible analysis (the only analysis in which it could be included). In contrast, the female late juvenile / young adult RPI-54 plots away from the other *Ouranopithecus* specimens (both bilateral and hemimandible analysis; Figure 3a–b). This might be partly due to its developmental stage in addition to sex differences in mandibular shape. In African apes, mandibular shape changes during growth, evident in different parts of the mandible (e.g., mandibular width, ramus). It has also been shown that corpus width changes with dental eruption (Daegling, 1996; Taylor, 2002; Taylor & Groves, 2003). RPI-54 is at a late stage of ontogeny (full eruption of M2) with moderate occlusal wear, suggesting that its mandibular shape should not differ greatly from that of adults. However, a small degree of ontogenetic variation cannot be excluded.

Only one *Ouranopithecus* specimen, RPI-391, could be included in our analysis of the ramus, limiting this analysis. This specimen shows a narrow gonial angle and a gonion positioned superiorly, resembling the shape of *Pongo*. However, it also exhibits some taphonomic distortion (flattening), which could have influenced the results. Our PCA showed substantial overlap in ramal morphology of the great apes, in contrast to a previous study that found a distinct shape in *Gorilla*, and clustering of *Pan* and *Pongo* (Terhune et al., 2014). However, in that study, 2D landmarks and semilandmarks were registered on different anatomical regions on the ramus than in this study, such as the coronoid process and mandibular notch. Due to the state of preservation of the only ramus specimen, RPI-391, we could not use the same

landmark set as Terhune et al. (2014). The differences in our results may therefore stem from the differences in our datasets.

In this study, we aimed to assess the degree of morphological variation in the mandibular shape of *Ouranopithecus*, compared to that observed in extant great apes. Based on the intra-specific Procrustes distances, *Ouranopithecus* shows somewhat greater inter-individual distances than the extant great apes, as these mostly fall at the highest extreme of the ranges of the extant apes for both the bilateral and hemimandible analysis. However, only one female specimen of *O. macedoniensis*, a late juvenile/young adult, could be included in the bilateral analysis, which lowers the statistical reliability. Moreover, the pairwise distances between the *Ouranopithecus* mandibles fall within the 95% probability interval of all pairwise distances of *Gorilla* in both the bilateral and hemimandible analysis, except for the Procrustes distance between specimens RPI-79 and RPI-56 (a female and a male, respectively) in the latter. The distances between the *Ouranopithecus* mandibles fall outside the respective pairwise distance ranges of *Pan* and *Pongo* in the bilateral analysis, while in the hemimandible analysis, three of the *Ouranopithecus* pairwise distances (RPI-79 and RPI-56; RPI-79 and RPI-75; RPI-56 and RPI-75) fall outside the 95% probability interval of *Pan* and *Pongo*. Significance tests on the mean differences between *O. macedoniensis* and the great apes indicate that differences with *Pan* and *Pongo* are significant, while those with *Gorilla* are not. This suggests that there is more mandibular shape variation in the small *Ouranopithecus* sample than in two of the three great apes, although limitations relating to sample size apply.

## 4.2 | Sexual dimorphism and size-related differences

Another aim of this study was to explore the degree of sexual dimorphism expressed in the shape and size of the mandible in *Ouranopithecus* and to compare this to sexual dimorphism present in the extant great apes. There were no significant male–female shape differences within *Gorilla* and *Pan* (except in hemimandible analysis). Still, there were significant differences between the sexes in mandibular corpus, symphysis, and ramus shape in *Pongo*. Our comparison of differences between male–female centroid means of bilateral and hemimandible analyses further indicates that sexual dimorphism in size is more strongly expressed in the larger great apes, *Gorilla* and *Pongo*, but is largely absent in *Pan*, a finding also supported by the significance tests. Our results are therefore consistent with other studies demonstrating that mandibular sexual size dimorphism is expressed only in the larger great apes, *Gorilla* and *Pongo*, including previous work using multivariate statistical analyses (Chamberlain & Wood, 1985; Robinson, 2003, 2012; Schmittbuhl et al., 2007; Singh, 2014; Taylor, 2006; Taylor & Groves, 2003). By comparison, *Ouranopithecus* shows the greatest differences between male and female centroid size means, suggesting it was more sexually dimorphic than the extant great apes. However, this result could be influenced by our small sample sizes. Based on the male–female centroid size pairwise differences in the mandibular and hemimandible analyses,

*Ouranopithecus* is more similar to *Pongo* than to *Gorilla* or *Pan* in its level of mandibular size dimorphism, although the *Ouranopithecus* values fall in the upper part of the *Pongo* range. Overall, our results suggest that the degree of mandibular size sexual dimorphism in *Ouranopithecus* may exceed that of *Pongo*, an interpretation that is in line with results from previous studies on the dentition (Koufos, de Bonis, & Kugiumtzis, 2016; Scott et al., 2009). Lastly, our correlation analyses between size and shape showed that PC1 is significantly correlated with size in all three shape analyses, with the degree of correlation varying from moderate to substantial. This suggests that size partly determines the morphology of these taxa, including *Ouranopithecus*, and contributes to the greater similarity in mandibular shape between *Ouranopithecus* and the two larger apes relative to *Pan*.

As mentioned in the introduction, *O. macedoniensis* shows a high level of dental size variation, which led some researchers to propose a two-species hypothesis (Kay, 1982; Kay & Simons, 1983). However, an alternative interpretation is that this variation is instead related to a high degree of sexual dimorphism, given that *Ouranopithecus* is characterized by morphological homogeneity in the dentition (Koufos, 1995; Koufos, de Bonis, & Kugiumtzis, 2016; Schrein, 2006; Scott et al., 2009). Moreover, a high degree of dental variation, exceeding the ranges expressed by the larger great apes, is also present within other Miocene species, such as *Proconsul major*, and *Lufengpithecus lufengensis* (Kelley & Etlar, 1989; Kelley & Plavcan, 1998; Scott et al., 2009; Uchida, 1996; Wood & Xu, 1991). Therefore, sexual dimorphism in the small *O. macedoniensis* sample may be elevated compared to the extant great apes, but is comparable to that described for other well-represented Miocene hominoids. As has been previously suggested, the most dimorphic extant taxa do not necessarily set the upper limits of variation in fossil primates (e.g., Kelley & Xu, 1991; Kelley, 1993; Scott et al., 2009).

Similar to many fossil specimens (see, e.g., Gingerich, 1983; Kidwell & Holland, 2002; Forey et al., 2004, and references therein), and despite our efforts to avoid distorted anatomical regions (e.g., use only of the undistorted anatomical side of RPI-79), the *Ouranopithecus* specimens might also be affected by taphonomic processes resulting in slight distortions and asymmetries, which may account for shape and (to a lesser extent) size variation observed in our sample. Finally, our sample includes a late juvenile/young adult fossil individual, which may have introduced a small level of ontogenetic variation. Despite these limitations, this study provides important new insights into the patterns of mandibular shape and size variation in *O. macedoniensis*.

## 5 | CONCLUSIONS

Our results, based on 3D geometric morphometrics and multivariate statistical analyses, show that mandibular shape can differentiate *Ouranopithecus macedoniensis* from the extant great apes. *O. macedoniensis* shows some shape similarities to the larger great apes, *Gorilla* and *Pongo*, a similarity probably due, in part, to a similar size. *O. macedoniensis* shows an elevated degree of morphological variation

compared to *Gorilla* and *Pongo*, notable given the small sample size but perhaps exaggerated somewhat by the inclusion in the small sample of a subadult individual. Sexual dimorphism in the mandibles of *O. macedoniensis* appears to be quite high, seemingly greater than in *Gorilla* and high even compared to *Pongo*, but this again is perhaps partly an artifact of small sample size.

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## CONFLICT OF INTEREST

The authors have no conflict of interests in the publication of this paper.

## AUTHOR CONTRIBUTIONS

**Melania Ioannidou:** Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (lead); writing – original draft (lead); writing – review and editing (lead). **George Koufos:** Conceptualization (supporting); funding acquisition (supporting); supervision (equal); writing – review and editing (supporting). **Louis de Bonis:** Conceptualization (supporting); supervision (supporting). **Katerina Harvati:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (lead); project administration (lead); resources (lead); supervision (lead); writing – review and editing (equal). Open access funding enabled and organized by Projekt DEAL.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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