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### RESEARCH ARTICLE

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## The arteries of the musculoskeletal system of siamangs, and a comparison with other hylobatids, greater apes, and humans

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### Abstract

Limited research on the gross anatomy of the blood vessels has been conducted on hylobatids, or lesser apes, so far. Here, we present a detailed study of the arteries of siamangs (Symphalangus) and compare our findings with data compiled from our previous studies as well as from the literature about other hylobatids, greater apes, and humans. In particular, a three-dimensional full-body computed tomography data set of a siamang neonate was analyzed in detail for this study, with notable findings in the head and neck, thorax, upper limb, abdomen and pelvis, and lower limb. Of the 62 arteries that we studied in detail, a total of 20 arteries that have never been described in detail in hylobatids are reported in this study. Key similarities to other apes differing from humans include the existence of a humeral common circumflex trunk and the origination of the dorsalis pedis from the posterior tibial artery or saphenous artery instead of the anterior tibial artery. Similarities to humans differing from other apes include the separation of the lingual and facial arteries and the origination of the profunda brachii from the brachial artery instead of the axillary artery. Our research and broader comparisons, therefore, contribute to knowledge about the soft tissues of hylobatids, other apes, and primates in general and facilitate a better understanding of the anatomical evolution and key differences and similarities among these taxa.

### KEYWORDS

apes, arteries, blood vessels, comparative anatomy, humans, hylobatids, lesser apes, primates, siamangs, soft tissues

### 1 | INTRODUCTION

The scientific literature on the arteries of primates, specifically hylobatids, is limited. While the musculoskeletal system of hylobatids has been studied extensively, not much is known about their arteries (reviewed in Diogo et al., 2012). However, studying the soft tissues of nonhuman primates, in particular apes, is crucial to illuminate our understanding of the differences and similarities between primate groups and therefore our own evolution. In 1999, Gibbs reviewed the very scarce information—mostly obtained from different authors

focusing on a certain specific anatomical region of the body– available for the arteries of hylobatids and concluded that indeed much was left to be studied concerning the blood vessels of the lesser apes (family Hylobatidae, including gibbons and siamangs).

Gibbs briefly described what other authors had written about the arteries of gibbons of the genus *Hylobates*, with just some remarks about siamangs (*Symphalangus*) (Gibbs, 1999). The only living siamangs are arboreal hylobatids native to the forests of Thailand, Indonesia, and Malaysia, from the species *Symphalangus syndactylus*. An author frequently cited in Gibbs' (1999) review of the blood vessels of hylobatids

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was Manners-Smith (1912), who wrote about the limb arteries of primates in general. Although not mentioned by Gibbs, Fitzwilliams (1905) described the musculoskeletal system and some of the arteries of Hylobates agilis. Other studies on the blood vessels of hylobatids cited by Gibbs illustrated just some specific arteries, such as the pulmonary artery (Nakakuki & Ehara, 1993) and cystic artery (Gordon, 1967). Some studies examined arteries of the head of gibbons (e.g., Diamond, 1991; Watts, 1934). Since Gibbs' 1999 review, only a few publications provided information about the blood vessels of hylobatids, such as the arterial supply of the pancreas (Shawuti et al., 2009) and the morphology of the heart and its vessels (Rung-ruangkijkrai et al., 2015). Interestingly, some of these studies documented noticeable variations among hylobatids: for instance, the Symphalangus individuals studied by Kawashima et al. (2008) had three arteries arising from the aortic arch like most humans have (brachiocephalic trunk and left common carotid and left subclavian arteries), while the Hylobates individuals described by Chapman (1900), Kawashima et al. (2008), Poynter (1916), and Rung-ruangkijkrai et al. (2015) only had two (left subclavian and either a bovine arch where the brachiocephalic artery shares a common origin with the left common carotid artery or truncus bicaroticus where the left common carotid artery originates from the brachiocephalic artery). This example stresses that one cannot simply presume that the arteries of siamangs are similar to those of gibbons—which as explained are moreover poorly studied as well -and therefore emphasises that detailed studies of the arteries of siamangs are crucially needed to know more about the phenotype of hylobatids and its differences and similarities to great apes and humans.

Because of this, and as Gibbs' (1999) review was carried out as a PhD thesis that remains unpublished to date, in the present paper we: (1) provide the first detailed, overall, analysis of the arteries of *Symphalangus*, and (2) then compare our findings with those reviewed by Gibbs for hylobatids and, importantly, also for Pan, *Gorilla*, *Pongo*, and *Homo*. Netter's human anatomy atlas served as an important reference for the anatomy of *Homo* (Netter, 2019). The female neonate specimen analyzed in this study is compared with data obtained for other hylobatids and other apes, including those noted in the Gibbs thesis. In particular, we were able to use a siamang specimen specifically prepared for the study of the blood vessels (Figure 1), which is ideal to visualize and describe the arteries associated with the musculoskeletal system of the whole body and to compare them with the scarce information available for other siamangs and for gibbons, as well as to great apes and humans.

### 2 | MATERIALS AND METHODS

The *Symphalangus* specimen is part of a zoological specimen collection for research on primate anatomy created by W. C. Osman Hill between 1930 and 1975 before the enforcement of CITES. The specimen, likely born from a captive mother, had a stillborn or a natural neonatal death like others in the collection, which was then given to the Royal College of Surgeons of England in 1976. The *Symphalangus* specimen comprises a complete body injected with a radiopaque material, likely radiopaque resin, as was used during the time of W. C. Osman Hill's research (Museum ref: RCSOM/OH/W098).

For this study, a full-body X-ray computed tomography of the female neonate was done (Figure 1). The acquisition took place using a Nikon Metrology HMX ST 225 (Nikon Metrology NV) with an UltraFocus static reflection tungsten target, set to 215 kV and 349 µA, filtered with 1 mm of tin. The recorded data consisted of 3142 projections of 354 ms each, with a frame averaging of 4 over a 360° rotation of the specimen. The computed tomographic reconstruction was performed using CT pro 3D 3 (Nikon Metrology), generating a 16-bit data set with an isotropic voxel size of 114.79  $\mu$ m. The data set was then visualized by using the software 3D Slicer Version 4.11.20210226: shift and the preset "CT-AAA" options were used to reveal the arteries in a three-dimensional (3D) space. Five tables were then made to summarize the information obtained for this siamang species, the information about the arteries of hylobatids, great apes and humans compiled by Gibbs (1999), and a few other papers published about the arteries of hylobatids that were not reviewed by Gibbs or that were published since the 1999 work (Tables 1-5). As Gibbs' (1999) thesis remains unpublished, for those people who want to consult it, we made it freely available under the "resources for researchers" items of the Visible Ape webpage (www. visibleape.com). Accordingly, apart from a column about the data drawn from other authors on the arteries of hylobatids, we included, in these tables, a separate column in which we show our observations of the Symphalangus arteries from the computed tomography scan, to highlight our observations versus those of other authors.

Furthermore, to more easily disseminate the information obtained in the present work about the arteries of siamangs to the readers and the broader public in general, coauthor J. S. Martin did the 3D reconstructions



**FIGURE 1** Rendering of the X-ray computed tomography data of the siamang individual described in this paper, which was injected with radiopaque material to reveal the cardiovascular system.

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TABLE 1 Differences between arteries of the head and neck of Homo, Hylobates, Pan, Gorilla, Pongo, and Symphalangus.

Arteries	Ното	Hylobates	Pan	Gorilla	Pongo	Symphalangus
External carotid	х	N/A	Х	х	х	Х
Superior thyroid	х	N/A	Х	х	х	Х
Superior laryngeal	Х	N/A	Х	N/A	N/A	х
Ascending pharyngeal	Х	N/A	Х	N/A	Х	х
Lingual	Х	N/A	Х	N/A	Х	х
Occipital	Х	N/A	х	N/A	Х	х
Facial	Х	N/A	Х	N/A	Х	х
Posterior auricular	Х	N/A	Х	N/A	Х	х
Superficial temporal	Х	N/A	Х	N/A	Х	х
Maxillary	Х	N/A	Х	N/A	Х	х
Inferior alveolar	Х	N/A	Х	N/A	Х	х
Infraorbital	Х	N/A	Х	N/A	Х	х
Deep temporal arteries	Х	N/A	Х	N/A	Х	х
Internal carotid	Х	х	Х	N/A	Х	х
Ophthalmic	Х	х	N/A	N/A	Х	х

Abbreviations: Abs, artery absent; N/A, no information available; X, artery present.

TABLE 2 Differences between arteries of the thorax of Homo, Hylobates, Pan, Gorilla, Pongo, and Symphalangus.

Arteries	Ното	Hylobates	Pan	Gorilla	Pongo	Symphalangus
Vertebral	Х	Х	Х	Х	Х	Х
Aorta	Х	х	Х	Х	Х	Х
Brachiocephalic trunk	Х	х	Х	Х	Х	Х
Left common carotid	Х	х	Х	Х	Х	х
Left subclavian	Х	х	Х	Х	N/A	Х
Internal thoracic	Х	N/A	Х	Х	N/A	х
Bronchial arteries	Х	N/A	Х	N/A	Х	Х
Posterior intercostal arteries	Х	N/A	Х	Х	Х	х
Lateral thoracic	Х	х	Х	Х	Х	Х
Thoracoacromial	Х	х	Х	Х	Х	х
Superior thoracic	Х	Abs	Х	Х	Abs	Abs

Abbreviations: Abs, artery absent; N/A, no information available; X, artery present.

shown in Figures 2-6. These 3D reconstructions are part of a project led by coauthor Rui Diogo, for our Visible Ape Project (VAP) website (www. visibleapeproject.com). The 3D mesh models were created with the 3D editor Zbrush (Pixologic, Inc.). The surface elements of the musculoskeletal system and the arteries were built by using the sculpting tools, and the uniform 3D structures were built by recalculating polygons of the interactive mesh. A standard color was used with light, shadow, material, and position configured before the model was rendered. The computed tomography scans from this study are included as one of the raw files kept on the VAP website (https://www.visibleapeproject.com): Rui Diogo will make this file and any other raw file kept on that website available to any person who requests it.

#### 3 RESULTS

Our observations of the arteries of the neck and head regions of Symphalangus are summarized in Table 1 and schematized in Figures 2-4. Here, we refer to just some of the key features, particularly those that our a posteriori comparisons revealed to be rather peculiar within hylobatids

TABLE 3	Differences between	arteries of the up	per limb of Hom	o, Hylobates, Pan,	Gorilla, Pongo,	and Symphalangus.
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Arteries	Homo	Hylobates	Pan	Gorilla	Pongo	Symphalangus
Axillary	Х	х	Х	Х	Х	Х
Anterior and posterior circumflex humeral arteries	Х	х	Х	Х	Х	Х
Brachial	Х	х	Х	Х	Х	Х
Profunda brachii	Х	х	Х	Х	Х	Х
Superior ulnar collateral	х	х	Х	х	х	х
Radial	х	х	Х	Х	Х	х
Palmar carpal arteries	х	х	N/A	х	х	х
Superficial palmar	Х	х	Х	х	х	х
Princeps pollicis	х	х	Х	х	х	х
Radialis indicis	х	х	Х	х	х	х
Ulnar	Х	х	Х	х	х	Х
Common interosseous	Х	Abs	Х	Abs	Abs	х
Anterior interosseous	х	х	Х	х	х	х
Posterior interosseous	Х	х	Х	х	х	х
Deep palmar	х	х	Х	х	х	х
Palmar metacarpal arteries	х	Х	х	х	Abs	х
Common palmar digital arteries	х	х	Х	Х	Х	х

Abbreviations: Abs, artery absent; N/A, no information available; X, artery present.

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Arteries	Homo	Hylobates	Pan	Gorilla	Pongo	Symphalangus
Abdominal aorta	х	Х	х	Х	Х	Х
Hepatic	х	х	Х	х	N/A	Х
Splenic	х	х	Х	х	х	Х
Renal arteries	х	N/A	Х	х	N/A	х
Internal iliac	х	N/A	Х	N/A	N/A	х
External iliac	х	х	Х	х	х	х
Inferior epigastric	Х	х	Х	Х	Х	Х

TABLE 4 Differences between arteries of the abdomen and pelvis of Homo, Hylobates, Pan, Gorilla, Pongo, and Symphalangus.

Abbreviations: Abs, artery absent; N/A, no information available; X, artery present.

or hominoids in general. The superior laryngeal artery appears to branch directly from the external carotid (Figure 6). The lingual and facial arteries are separate branches (Figure 7). The internal carotid artery has two branches near its origin from the common carotid artery going posteriorly, with one going superiorly and the other going inferiorly (Figure 9).

Our observations of the arteries of the thoracic region of *Symphalangus* are summarized in Table 2. The aortic arch gives off three branches including the brachiocephalic trunk, left common carotid, and left subclavian. Only eight pairs of posterior intercostal arteries were seen derived from the thoracic aorta. However, there may be more posterior intercostal arteries, as the computed

tomography reconstruction may not have fully reconstructed all of these arteries. The lateral thoracic artery was an independent branch of the axillary artery, and clavicular, acromial, and deltoid branches of the thoracoacromial trunk are present (Figure 10). Our specimen did not seem to have a superior thoracic artery.

Data on the arteries of the upper limb are displayed in Table 3 and shown in Figure 5. The anterior and posterior circumflex humeral arteries arise from a common circumflex trunk (Figure 10). The posterior circumflex humeral is larger than the anterior circumflex humeral, and the profunda brachii (deep humeral artery) originates from the brachial artery. The superficial palmar artery—also known as

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TABLE 5	Differences between	arteries of the	e lower limb	of Homo,	Hylobates, Pan	, Gorilla, F	ongo, and Symphalangus.
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Arteries	Ното	Hylobates	Pan	Gorilla	Pongo	Symphalangus
Femoral	Х	х	Х	х	N/A	Х
Medial circumflex femoral	Х	N/A	Х	N/A	N/A	Х
Profunda femoris	Х	х	х	Х	Х	Х
Lateral femoral circumflex	Х	х	х	Х	Х	Х
Popliteal	Х	х	Х	Х	Х	Х
Anterior tibial	Х	х	Х	Х	Х	х
Dorsalis pedis	Х	N/A	х	Х	Х	Х
Posterior tibial	Х	х	Х	Х	Х	х
Fibular	Х	х	х	Х	Х	Х
Medial plantar	Х	х	Х	N/A	Х	х
Lateral plantar	Х	Abs	Х	Х	Х	Abs
Plantar metatarsal arteries	Х	x	Х	Х	N/A	Х

Abbreviations: Abs, artery absent; N/A, no information available; X, artery present.



FIGURE 2 Frontal view of our three-dimensional reconstruction of the arteries of the head and neck of the siamang.

the superficial palmar branch of the radial artery-appears to be present in the Symphalangus specimen, but it is unclear if it continues to complete the superficial palmar arch. The common interosseous artery is present (Figure 11), arising from the brachial artery. The deep palmar arch is formed mainly by the deep palmar ramus of the ulnar artery and completed by the radial artery (Figure 12). The radial contribution is slight, with the main vessel being the deep palmar

ramus of the ulnar artery. The palmar metacarpal arteries originate from the deep palmar arch. The common palmar digital arteries appear to supply adjacent sides of digits II-V. The common palmar digital arteries bifurcate into proper palmar digital arteries (Figure 12). The most ulnar common palmar digital artery in Symphalangus does not bifurcate, but is seen to give off another common palmar digital artery that bifurcates to digits IV and V.





FIGURE 3 Superficial lateral view of our three-dimensional reconstruction of the arteries of the head and neck of the siamang.



FIGURE 4 Deep lateral view of our three-dimensional reconstruction of the arteries of the head and neck of the siamang.

Data on the arteries of the abdomen and pelvic region are displayed in Table 4. The celiac trunk is not identifiable, but the common hepatic artery and splenic artery appear to have the same origination. The short gastric branches are present. The left gastro-omental artery originates from the splenic artery and anastomoses with the right gastro-omental artery. The right gastro-omental artery originates from the common hepatic artery. The right and left renal arteries are present as is the internal iliac artery (Figure 15). The inferior epigastric artery is seen as a branch of the external iliac artery (Figure 15). Interestingly, in *Symphalangus*, another unknown artery is seen headed superiorly branching from the same vessel that gives rise to the inferior epigastric artery (Figure 15).

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FIGURE 5 Frontal view of our three-dimensional reconstruction of the arteries of the upper limb of the siamang.



FIGURE 6 Frontal view of our three-dimensional reconstruction of the arteries of the lower limb of the siamang.



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**FIGURE 7** Lateral view of the (A) common carotid artery, (B) internal carotid artery, (C) external carotid artery, (D) superior laryngeal artery, (E) superior thyroid artery, (F) facial artery, (G) lingual artery, (H) maxillary artery, and (I) posterior auricular artery of the siamang.

Data on the arteries of the lower limb are displayed in Table 5 and shown in Figure 6. The medial circumflex femoral artery is a branch of the femoral artery. The profunda femoris (deep femoral artery) originates from the femoral artery, with the lateral femoral circumflex being a branch of the profunda femoris, which divides into three branches. The lateral femoral circumflex artery itself divides into ascending and descending branches (Figure 16). The popliteal artery appeared to give off a common branch for the anterior tibial and fibular arteries. The posterior tibial artery appears to originate more proximally from the superficial femoral artery or subsartorial artery. The superficial femoral artery is the segment between the branching point of the deep femoral artery and the adductor hiatus. Given the location, it is possible that this posterior tibial artery is the saphenous artery, or the saphenous branch of the descending genicular artery, as it will be discussed below. The saphenous artery is labeled in our observations as the posterior tibial artery because of its supply of the medial plantar artery (Figure 18). The dorsalis pedis appears to be a branch of the posterior tibial, but it may potentially be a branch of the saphenous artery (see Section 4 below). The posterior tibial does not have a lateral plantar artery, and the medial plantar artery completes the plantar arch (Figure 18). There are four plantar metatarsal arteries given off from the plantar arch (Figure 18).

### 4 | DISCUSSION

All the arteries that could be identified in the specimen by using the computed tomography scans are noted in Tables 1–5. Those structures not included in the tables were not identifiable. Those not noted in the results and discussions but that are included in the table have patterns that are identical to those of other hominoids.

The main limitation of this study is that only one specimen of *Symphalangus* has been analyzed, which makes the observed results specific to this individual, and thus limits knowledge about



**FIGURE 8** Lateral view of the (A) posterior deep temporal artery, (B) anterior deep temporal artery, (C) ophthalmic artery, and (D) facial artery of the siamang.

intraspecific variation. However, regarding variation within hylobatids, and within hominoids in general, the comparisons with other hylobatids and hominoids previously described in the literature partially address this limitation, although future detailed vascular studies of more hylobatids, and other apes, are obviously much needed. Additionally, the computed tomography reconstruction may not fully reconstruct the paths of certain arteries, as noted by the unidentified observed arteries in this study. However, having said that, this is the most detailed study done to this day about the blood vessels of *Symphalangus*, so it is a crucial contribution to the knowledge about the blood vessels of hylobatids and other apes.

In fact, our observations of *Symphalangus* reveal, for instance, new details about the branches of the external carotid artery on the neck and head regions (Table 1 and see also Figures 2–4). Notably, while the superior laryngeal artery appears to branch directly from the external carotid artery in this specimen, it arises from the superior thyroid artery in *Pan* and *Homo* (Figure 7) (Gibbs, 1999; Netter, 2019). As it often occurs in *Homo, Symphalangus* has the lingual and facial arteries as separate branches instead of joined together as a linguofacial trunk, as it commonly occurs in *Pan* and *Pongo* and in about 20% of *Homo* according to Gibbs (Figure 7) (Gibbs, 1999; Netter, 2019). Unlike the two differently sized arteries of *Pongo*, the deep temporal arteries appear to be equal in size in *Symphalangus* like in *Pan* and *Homo* (Figures 4 and 8) (Gibbs, 1999; Netter, 2019).

Regarding the thoracic region, the aortic arch gives off three branches including the brachiocephalic trunk, left common carotid, and left subclavian like it often occurs in *Pan, Gorilla*, and *Homo* (Gibbs, 1999; Netter, 2019). This is unlike most orangutans (*Pongo*), in which it gives off only the brachiocephalic trunk and left subclavian arteries (Gibbs, 1999) and unlike gibbons, which appear to have a common trunk for the brachiocephalic and left common carotid artery or have the left common carotid artery originate from the brachiocephalic artery as described by Chapman (1900), Kawashima et al. (2008), Poynter (1916), and Rung-ruangkijkrai et al. (2015). Only eight pairs of posterior intercostal arteries were seen derived from the thoracic aorta, but as noted above there may be more posterior

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FIGURE 9 Lateral view of the (A) common carotid artery, (B) external carotid artery, (C) internal carotid artery, (D) unknown artery heading inferiorly, and (E) unknown artery headed superiorly to the siamang.



FIGURE 11 Superior anterior view of the (A) brachial artery, (B) common interosseous artery, (C) ulnar artery, and (D) radial artery of the siamang



FIGURE 10 Anterior view of the (A) axillary artery, (B) internal thoracic artery, (C) lateral thoracic artery, (D) common circumflex trunk, and (E) brachial artery of the siamang.

intercostal arteries, as the computed tomography reconstruction may not have fully reconstructed all of these arteries. The lateral thoracic artery is a branch of the thoracoacromial trunk in Hylobates (Gibbs, 1999): interestingly in Symphalangus this was not the case, as the lateral thoracic artery was an independent branch of the axillary artery (Figure 10) as it often occurs in Homo, Pan, and Gorilla (Gibbs, 1999; Netter, 2019). Clavicular, acromial, and deltoid branches of the thoracoacromial trunk are present in Symphalangus like it is commonly the case in Pan, Pongo, and Homo (Gibbs, 1999; Netter, 2019). While the pectoral branch is present in most humans and some chimpanzees (Pan), it is absent in the Symphalangus specimen as it is reported to be in Gorilla (Gibbs, 1999; Netter, 2019). Unlike Homo, Pan, and Gorilla, Symphalangus did not seem to have a superior thoracic artery, like in Pongo (Gibbs, 1999; Netter, 2019).

Concerning the upper limb, while the anterior and posterior circumflex humeral are usually independent branches of the axillary artery in Homo, they arise from a common circumflex trunk in the Symphalangus specimen as is commonly found in other apes (Figure 10) (Gibbs, 1999; Netter, 2019). The common circumflex trunk is also a relatively frequent variation in Homo. The posterior

circumflex humeral is larger than the anterior circumflex humeral like is often the case in Homo, Pan, and Gorilla (Gibbs, 1999). The profunda brachii (deep humeral artery) originates from the brachial artery like in Pan and Homo, in contrast to what usually happens in Hylobates and other apes, in which it originates from the axillary artery (Gibbs, 1999; Netter, 2019). Unlike other apes and most humans, Gibbs notes that the superficial palmar artery may be absent in Hylobates. The superficial palmar artery appears to be present in the Symphalangus specimen as noted above, but it is unclear if it continues to complete the superficial palmar arch as it usually happens in Homo, Pan, and Pongo, or ends instead in the thenar muscles as reported in Gorilla and gibbons that do have this artery (Gibbs, 1999; Netter, 2019). While the common interosseous artery of the forearm is absent in Hylobates according to Gibbs, it is present in the Symphalangus specimen (Figure 11), arising from the brachial artery as it sometimes occurs in Homo and Pan (Gibbs, 1999). The common interosseous artery arises mainly from the ulnar artery in Homo (Netter, 2019). The deep palmar arch is formed mainly by the deep palmar ramus of the ulnar artery and completed by the radial artery (Figure 12) is similar to other apes according to Gibbs, but differs from Homo, in which the deep palmar arch is formed mainly by the radial artery with contribution from the ulnar artery (Netter, 2019). While Gibbs notes that the palmar metacarpal arteries run only into the second and third spaces (between the metacarpals), they appear to run in the second, third, and fourth spaces in Symphalangus as is the case in some of Pan, Gorilla, and Homo (Gibbs, 1999; Netter, 2019). The palmar metacarpal arteries originate from the deep palmar arch as is commonly the case in Gorilla and Homo unlike in Pan where they originate from the radial artery (Figure 12) (Gibbs, 1999; Netter, 2019). The common palmar digital arteries appear to supply adjacent sides of digits II-V like in some chimpanzees and in most humans (Figure 12) (Gibbs, 1999; Netter, 2019). The common palmar digital arteries bifurcating into proper palmar digital arteries also occur in Homo (Figure 12) (Netter, 2019). However, the most ulnar common palmar digital artery in Symphalangus does not bifurcate but is seen to give off another common palmar digital artery that bifurcates to digits IV and

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**FIGURE 12** Palmar view of the (A) ulnar artery, (B) deep palmar arch, (C) common palmar digital arteries, (D) proper palmar digital arteries, (E) palmar metacarpal artery, and (F) princeps pollicis.

V instead of originating from the palmar arch as would be seen in *Homo* (Netter, 2019).

Regarding the pelvic region, the splenic artery is present in *Symphalangus* as it usually is in other apes and *Homo* (Figure 13) (Gibbs, 1999; Netter, 2019). The short gastric branches are present as in *Pan, Pongo*, and *Homo* (Figure 13) (Gibbs, 1999; Netter, 2019). The right gastro-omental artery originates from the common hepatic artery, which is similarly observed in a specimen of *Hylobates lars* (Shawuti et al., 2009). The right and left renal arteries are present as is usually the case in *Pan, Gorilla*, and *Homo* (Figure 14) (Gibbs, 1999; Netter, 2019). The inferior epigastric artery is seen as a branch of the external iliac artery as is usually the case in other apes and *Homo* (Figure 15) (Gibbs, 1999; Netter, 2019). Interestingly, as noted above in *Symphalangus*, another unknown artery is seen headed superiorly branching from the same vessel that gives rise to the inferior epigastric artery (Figure 15).

Lastly, concerning the lower limb, the medial circumflex femoral artery being a branch of the femoral artery is unlike in most of Pan, in which it is the branch of the external iliac artery, and in humans, in which it is the branch of the profunda brachii (deep femoral artery) (Gibbs, 1999; Netter, 2019). The profunda femoris (deep femoral artery) originates from the femoral artery as in most other apes and humans (Figure 16) (Gibbs, 1999; Netter, 2019). The lateral femoral circumflex is a branch of the profunda femoris, which divides into three branches, as it commonly happens in Pan, Pongo, and Homo (Gibbs, 1999; Netter, 2019). The lateral femoral circumflex artery itself divides into three branches in Hylobates, but as noted above only the ascending and descending branches were observed in Symphalangus (Figure 16) (Gibbs, 1999). While Gibbs notes that the popliteal artery divides into the anterior and posterior tibial branches in Hylobates like it usually occurs in Gorilla, Pongo, and Homo as shown by Netter, the Symphalangus specimen's popliteal artery appeared to give off a common branch for the anterior tibial and fibular arteries, like



**FIGURE 13** Superior anterior view of the (A) splenic artery and (B) short gastric branches of the siamang.



**FIGURE 14** Posterior oblique view of the (A) abdominal aorta, (B) renal arteries, (C) inferior vena cava, and (D) renal veins.

in Pan (Figure 17). However, unlike Pan where the posterior tibial artery originates from the popliteal artery, the posterior tibial artery in Symphalangus appears to originate more proximally from the superficial femoral artery, or subsartorial artery, where the descending genicular artery would typically be located in Homo (Gibbs, 1999; Netter, 2019). As explained above, given the location of the structure that we labeled as the posterior tibial artery, this structure might actually be the saphenous artery or the saphenous branch of the descending genicular artery in Homo as described by Netter, which is consistent with Gibbs' notes that the saphenous artery originates from the femoral artery in Hylobates and other apes instead of the descending genicular artery in Homo. Hence, it should be noted that the saphenous artery is not found in Homo. However, this structure was labeled in our observations as the posterior tibial artery because of its supply of the medial plantar artery (Figure 18). While the dorsalis pedis is usually the terminal branch of the anterior tibial artery in Homo, it appears to be a branch of the posterior tibial as it sometimes is in chimpanzees (Gibbs, 1999; Netter, 2019). However, it may potentially be a branch of the saphenous artery, which is consistent

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**FIGURE 15** Anterior view of the (A) internal iliac artery, (B) external iliac artery, (C) inferior epigastric artery, (D) unknown artery headed superiorly, and (E) internal iliac vein of the siamang.



**FIGURE 18** Plantar view of the (A) medial plantar artery, (B) deep plantar arch, and (C) plantar metatarsal arteries of the siamang.



**FIGURE 16** Medial view of the (A) femoral artery, (B) deep femoral artery (profunda femoris), the (C) ascending and (D) descending branches of the lateral femoral artery, and (E) superficial femoral artery of the siamang.



**FIGURE 17** Medial view of the (A) superficial femoral artery, (B) posterior tibial artery originating proximal to the (C) popliteal artery and the common branch for the (D) anterior tibial and (E) fibular artery of the siamang.

with Gibb's notes, being a feature found in *Gorilla* and *Pongo*, as well as in *Pan*. The posterior tibial does not have a lateral plantar artery unlike most other apes and humans (Gibbs, 1999; Netter, 2019). Unlike the usual configuration in *Pan*, *Pongo*, and *Homo*, in *Symphalangus* the medial plantar artery completes the plantar arch (Figure 18) (Gibbs, 1999). In *Homo*, Netter notes that the medial plantar artery gives off superficial and deep branches. However, similarly to *Pan* and *Homo*, there are four plantar metatarsal arteries given off from the plantar arch in *Symphalangus* (Figure 18) (Gibbs, 1999; Netter, 2019).

In summary, from these comparisons it can thus be said that the present paper provides key new observations not only for siamangs but for hylobatids in general, as these observations include data for several arteries never studied in detail in this lesser ape. Our new observations on the head and neck region of Symphalangus include the presence of separate lingual and facial arteries and the origin of the superior laryngeal artery directly from the external carotid artery, contrary to what often happens in other apes and humans. Our new observations on the thoracic region of Symphalangus include the existence of the internal thoracic artery, bronchial arteries, posterior intercostal arteries, and a case in which the lateral thoracic artery may be seen as a branch of the axillary artery instead of the thoracoacromial artery as in Hylobates. Our novel observations on the upper limb in Symphalangus include the existence of a common circumflex trunk, the origination of the profunda brachii from the brachial artery, and the existence of the common interosseous artery. Lastly, our new observations on the abdomen and pelvic region in Symphalangus include the existence of renal arteries and the internal iliac artery, and for the lower limb in Symphalangus include the existence of a posterior tibial artery that has the origination of the saphenous artery and the supply of both the dorsalis pedis and the medial plantar artery making up the plantar arch.

Regarding the results of our comparison between *Symphalangus* and other apes and humans, the data gathered by us in Tables 1–5 points out some interesting patterns. For instance, some patterns are

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commonly present in all these taxa. This includes, for the head and neck region, the fact that all apes and Homo usually have an external carotid artery and superior thyroid artery. For the thorax, all apes and Homo usually have a vertebral artery, aorta, brachiocephalic artery, left common carotid artery, posterior intercostal arteries, lateral thoracic artery, and thoracoacromial trunk. For the upper limb, all apes and Homo commonly have the axillary artery, anterior and posterior circumflex arteries, brachial artery, profunda brachii, superior ulnar collateral, radial artery, superficial palmar artery, princeps pollicis, radialis indicis, ulnar artery, anterior interosseous, posterior interosseous, deep palmar artery, and common palmar digital artery. The posterior circumflex humeral artery is larger than the anterior circumflex humeral artery in Symphalangus like is often the case in Homo, Pan, and Gorilla. For the abdomen and pelvic region, all apes and Homo usually have an abdominal aorta, splenic artery, external iliac artery, and inferior epigastric artery. The inferior epigastric artery is seen as a branch of the external iliac artery in Symphalangus, as is usually the case in all other apes and Homo. The profunda femoris, lateral circumflex artery, popliteal artery, anterior tibial artery, posterior tibial artery, and fibular artery are commonly present in all apes and Homo.

Interestingly, *Symphalangus* is similar to other apes but different from *Homo* in two key areas. First, while the anterior and posterior circumflex humeral arteries are often independent branches from the axillary artery in *Homo*, they arise from a common circumflex trunk in *Symphalangus* and most other apes. Second, while the dorsalis pedis usually originates from the anterior tibial artery in *Homo*, it appears to originate from the posterior tibial in *Symphalangus*, as it does in some chimpanzees, or from the saphenous artery, as it usually does in *Gorilla and Pongo* and in some chimpanzees.

Importantly, the arteries of *Symphalangus* are different from those of other apes but similar to *Homo* in some other ways. Like most *Homo* and unlike *Pan* and *Pongo*, *Symphalangus* has the lingual and facial arteries as separate branches of the external common carotid artery, instead of joined together as a linguofacial trunk (Figure 7). Also, the profunda brachii originates from the brachial artery like it usually does in *Pan* and *Homo*, but it usually originates from the axillary artery in *Hylobates*, *Gorilla*, and *Pongo*.

These examples stress the importance of mosaic evolution in primates, and even a single ape group such as the lesser apes, thus highlighting a particularly complex evolutionary history of the soft tissues, as has been described for muscles (see, for instance, review by Diogo & Wood, 2012). Such examples, and the present work in general, thus further emphasize the importance of studying soft tissues, in particular nonmuscular ones, as we can only fully understand the anatomical evolution of primates, and thus of our own lineage, when such a broader, more inclusive comparative analysis is done. In particular, detailed studies of the nerves and blood vessels, and particularly the veins, of apes, and of primates in general, are crucially needed. We hope this study will help pave the way—and motivate other researchers—to undertake such studies of such nonmuscular soft tissues of nonhuman primates.

### AUTHOR CONTRIBUTIONS

Laraine Cheung: Formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (lead); writing—original draft (lead); writing—review and editing (lead). Jose S. Martin: Conceptualization (equal); investigation (equal); methodology (equal); software (equal); visualization (equal). Nicole Barger: Conceptualization (equal); investigation (supporting); methodology (equal); project administration (supporting); software (equal); supervision (equal); writing—review and editing (equal). Carina Phillips: Data curation (lead); methodology (equal); resources (equal). Vincent Fernandez: Software (equal); visualization (equal). Rui Diogo: Conceptualization (lead); funding acquisition (equal); methodology (equal); project administration (lead); supervision (equal); writing—review and editing (lead).

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### DATA AVAILABILITY STATEMENT

The data that support this study are openly available from the Visible Ape Project at https://www.visibleapeproject.com, upon request to the corresponding author, Rui Diogo.

### PEER REVIEW

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