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ORIGINAL ARTICLE

Evolutionary transformation of the cervicobrachial plexus in the colugo (Cynocephalidae: Dermoptera) with a comparison to treeshrews (Tupaiidae: Scandentia) and strepsirrhines (Strepsirrhini: Primates)

What is the most important factor related to the specialised morphology of the cervicobrachial plexus in the colugo: its gliding locomotion, phylogenetic constraint, or semi-elongated neck?

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Four cervicobrachial plexuses from two colugos (Dermoptera), which are gliding mammals with semi-elongated necks, were dissected with imaging analysis and compared with those in its relatives, 12 sides of six treeshrews (Scandentia) and 32 sides of 16 strepsirrhines (Primates), for considering of its evolutionary constraint and functional adaptation. (1) The relative cervical length in the colugos was significantly longer than those in the others, regardless of the number and proportion of vertebrae. (2) In all examined colugos, the cervical plexus exhibited broader cervical root segments comprising the hypoglossal (N. XII) and first to fifth cervical (C1–C5) nerves, whereas the brachial plexus exhibited concentrated segments comprising C6 to the first thoracic nerve (T1) and part of T2. (3) On the other hand, the cervical plexus composed of N. XII and C1–C4 and the brachial plexus composed of C5–T1(2) were formed in all treeshrews (12/12 sides, 100.0%) and most strepsirrhines (27/32 sides, 84.4%) as seen in most terrestrial placental mammals. (4) Similar root segments of broader cervical and concentrated brachial plexuses were found in five sides of three strepsirrhines (15.6%), which are species with somewhat longer necks than the other strepsirrhines and treeshrews. Based on present and previous reports on elongated and shortened neck mammals, the modified root segments of the cervicobrachial plexus in the colugo appears to be related more to neck length than to its ecological habit, specialized locomotion, or any phylogenetic constraint. (Folia Morphol 2012; 71, 4: 228–239)

Key words: colugo, brachial plexus, cervical plexus, cervicobrachial plexus, functional anatomy, treeshrew, strepsirrhine

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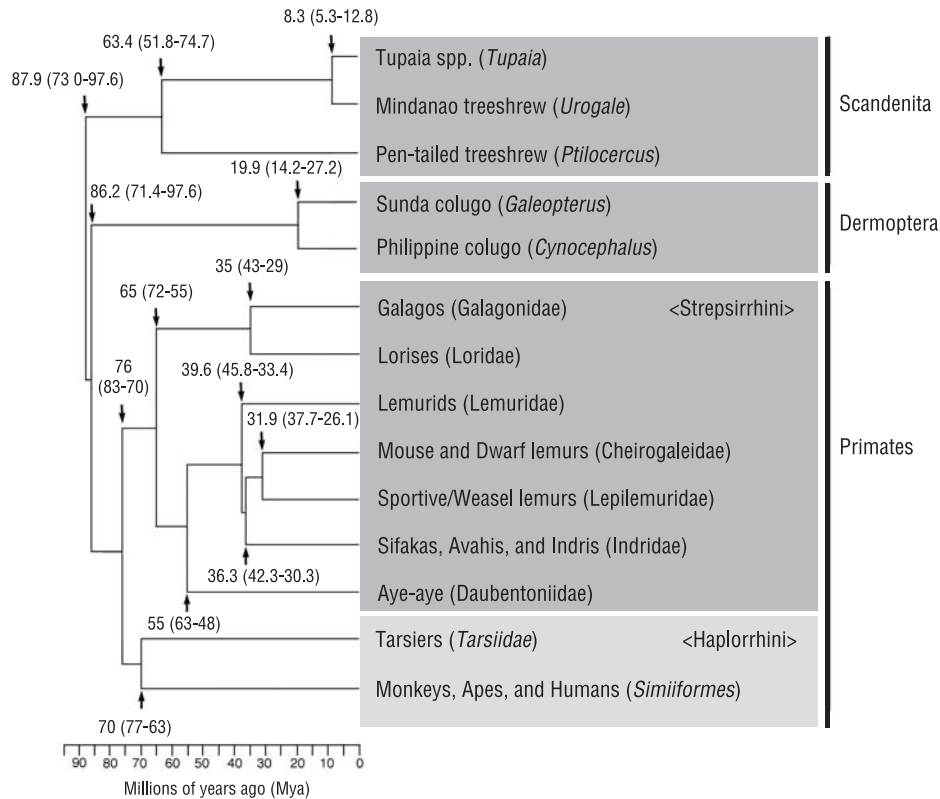
Figure 1. Phylogenetic relationship among the treeshrews (Scandentia), colugos (Dermoptera), and primate lineages based on recent molecular studies [17, 19, 33, 41, 61]

INTRODUCTION

The colugo, or flying lemur (Dermoptera), is a unique mammal adapted for aerodynamics. It also holds a key phylogenetic position as one of the primate relatives (Fig. 1) [17, 19, 28, 33, 41, 43, 44, 61, 74].

To date, research on the colugo has included morphological research on its muscles [40]; variations in vertebrae [11]; systematic anatomy [38]; skeleton [56]; skeleton, muscles, brain, and internal organs [5]; external morphology [51]; genital organs [20]; general anatomical characters [14]; hand morphology [1]; cranial vessels [73]; vomeronasal organ [2]; skull [58]; head and neck muscles [7]; and forelimb muscles [8].

Importantly, Leche [38] described in detail the skeleton, muscles, nervous system, and internal organs of the colugo using four specimens. Although the brachial plexus is a key structure on account of its functional adaptation, the morphology of the cervicobrachial plexus in the colugo was reported in only one case by Leche [38]. Therefore, it remains unclear whether this reported morphology on the cervicobrachial plexus in the colugo is typical. This insufficient anatomical information seems to be derived from the reason why it tends to evade capture for the purpose of research on arboreal and nocturnal mammals having a specialised ability to glide.

Moreover, it is also unclear that the evolutionary transformation of the cervicobrachial plexus among three groups, even in a long anatomical history, although numerous excellent anatomical researches on the treeshrews have been conducted from systematic, biological anthropological, or functional morphological viewpoints [4, 6, 9, 13, 16, 21, 30–32, 35–37, 55, 59, 60, 62] in addition to more tremendous morphological researches in strepsirrhines.

Consequently, the cervicobrachial plexus in the colugo is important for the following reasons:

1. *Phylogenetic relationship:* Because a detailed description of the human anatomy was originally the basis for anatomical terminology, the morphology of the colugo as a primate relative is important with respect to its recent molecular phyletic position (Fig. 1) [19].

2. *Adaptation for gliding:* Previously grouped with bats (Chiroptera), the colugo is an arboreal gliding creature. Because recent anatomical studies have shifted focus from the classical, evolution-

based anatomical description to functional morphology, the structure of somatic structures may have been modified through functional requirements [12, 39]. Therefore, it is necessary to examine the cervicobrachial plexus, which acts as a control system for the unique gliding forelimb.

3. *Adaptation for the semi-elongated neck:* Because the cervical vertebrae in almost all mammals are fixed at seven, the evolutionary and developmental specialisations of cervical variation in number have been recently discussed in sloths [3, 15, 48], and most mammals with seven cervical vertebrae are a suitable model for considering the transformation of the surrounding structures affected by the cervical length. Morphological changes in the cervicobrachial plexus of long-necked mammals, such as the giraffe and okapi, have been paid little attention, and the colugo is no exception. These changes should therefore be investigated.

This study aimed to examine and record the detailed anatomy of the cervicobrachial plexus in the colugo, and to consider the relationship between morphological changes in the cervicobrachial plexus and the three above-mentioned factors by comparison with its relatives: strepsirrhines and treeshrews (Table 1).

MATERIAL AND METHODS

In total four colugos, seven treeshrews, and 16 strepsirrhines were used for this study, as shown in Table 1. All specimens were fixed in 10% formalin and preserved in 10% alcohol obtained from several natural history museums and universities.

In order to obtain the topographical anatomy information, two of four colugos, five of seven treeshrews, and 13 of 16 strepsirrhines were examined by helical computed tomography (CT) analysis (Emotion; Siemens, MI, USA) in the National Museum of Natural History, Smithsonian Institution. Tube voltage, current, and slice width were set at 130 kV, 80 mA, and 1.0 mm, respectively. Cross-sectional images were reconstructed at 0.3 mm increments and transferred from DICOM to TIF formats using commercial software (The OsiriX; the OsiriX Foundation, Geneva, Switzerland).

Thereafter, four cervicobrachial plexuses from two skinned Philippine colugos (*Cynocephalus volans*: FM56532, FM56510), 12 cervicobrachial plexuses from six treeshrews, and 32 cervicobrachial plexuses from 16 strepsirrhines, with surrounding structures, were examined using forceps designed for optic surgery (Dumont #4; World Precision Instruments, FL, USA) and

a stereomicroscope (XTZ series zoom stereo microscope; Alltion Co., Ltd, Guangxi, China). In this anatomical examination in the colugos, innervations to the cutaneous muscles and membrane (patagium) were unclear because the specimens were skinned. The sequential steps of dissection were documented by detailed sketches and/or digital images taken using a Canon digital camera (Canon IXY digital 800IS; Tokyo, Japan). The anatomical terminology applied to the muscles and nerves mainly followed the previous references of Leche [38] and Chapman [5].

The protocol for the present research did not include any specification regarding approval from the Ethics Committee of our university (Toho University, No. 23011). The present work conformed to the provisions of the 1995 Declaration of Helsinki (revised in Edinburgh, 2000; http://www.wma.net/e//policy/17-c_e.html).

RESULTS

Specialised structures in colugos

The most outstanding specialised structure in the colugo is the patagium, with the ratio of its length to whole body size being greater than that of any other patagiate mammal (Fig. 2A, B). It is divided on each side into three well-developed parts and one additional part, the interdigital patagium. The three well-developed parts are recognised as the propatagium, located between the neck and forelimb; the palatopatagium or plagiopatagium, located between the fore- and hindlimbs; and the uropatagium, located between the hind limb and tail. Although the cutaneous muscles within the patagium are usually difficult to recognise by CT examination, the single coracohumerocutaneous muscle (fold), which acts as a support system for the patagium, was easily captured by both the naked eye and CT examination in our study (arrowheads in Fig. 2A, B).

Computed tomography examination of skeletal information including neck length

Table 2 summarises the number and length of axial vertebrae.

In the examined specimens, the presacral vertebrae in both species (Sunda and Philippine) colugos and all treeshrews exhibit constantly 7 cervical (CV), 13 thoracic (TV), and 6 lumbar (LV) vertebrae. On the other hand, presacral vertebrae except 7CV in strepsirrhines show the anatomical diversity within normal variation as shown in Table 2 [45, 53].

Table 1. Examined materials

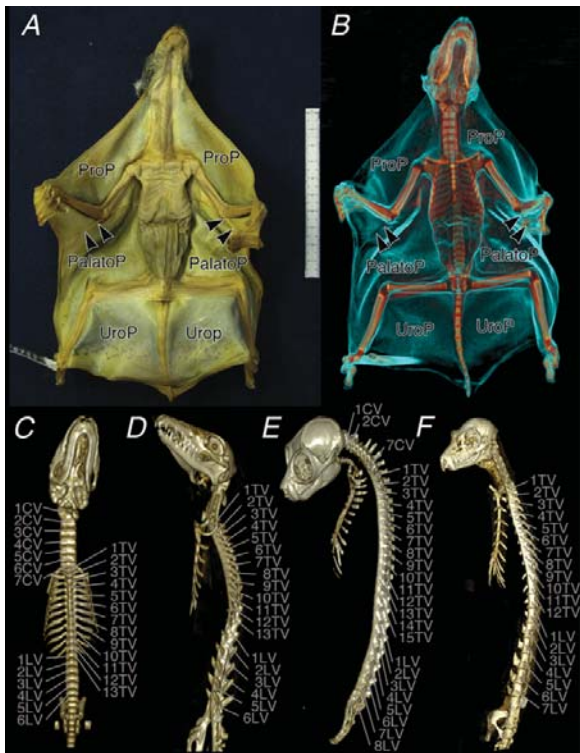| Species*	Ecological habit	Specimen no.	Sex	Stage (CRL)	Institution**	ID	CT	Dissection
(1) Colugo								
Family Cynocephalidae								
Sunda colugo (*Galeopterus variegatus*)	Arboreal, gliding	No. 1	F	Infant	USNM	US317290	o	o
Philippine colugo (*Cynocephalus volans*)	Arboreal, gliding	No. 2	M	Infant	USNM	US458984	o	o
		No. 3	?	Juvenile	FMNH	FM56532		o
		No. 4	?	Juvenile	FMNH	FM56510		o
Total: 4 specimens								
(2) Treeshrew								
Family Tupaiidae								
Common treeshrew (*Tupaia glis*)	Terrestrial/arboreal	No. 5	M	Adult (12.3 cm)	USNM	Thor.1963-1	o	o
		No. 6	F	Adult (11.4 cm)	USNM	Thor.1963-2	o	o
		No. 7	?	Adult	USNM	US-A2173	o	
Terrestrial treeshrew (*Tupaia tana paitana*)	Terrestrial/arboreal	No. 8	M	Adult (17.4 cm)	USNM	US546343	o	o
		No. 9	M	Adult (17.8 cm)	USNM	US339662	o	o
		No. 10	F	Adult (18.2 cm)	USNM	US582439		o
Philippine treeshrew (*Urogale everetti*)	Arboreal/terrestrial	No. 11	M	Adult (17.1 cm)	FMNH	FM61406		o
Total: 7 specimens								
(3) Strepsirrhini								
Family Lorisidae (Gray, 1821)								
Slow loris (*Nycticebus coucang*, Boddaert 1785)	Arboreal	No. 12	F	Sub-adult	DMU	N/A	o	o
		No. 13	M	Adult (25.7 cm)	USNM	US502559	o	o
Potto (*Perodicticus potto*, Muller 1766)	Arboreal	No. 14	M	Sub-adult (29.7 cm)	USNM	US502567	o	o
Family Galagidae (Gray, 1825)								
Brown greater galago (*Otolemur crassicaudatus*, E. Geoffroy 1812)	Arboreal	No. 15	F	Adult (25.6 cm)	USNM	US502569		o
Northern (small-eared) greater galago (*Otolemur gametti pangariensis*, Ogilby 1838)	Arboreal	No. 16	F	Infant (11.1 cm)	USNM	US540881	o	o
		No. 17	F	Infant (12.8 cm)	USNM	US540885	o	o
Senegal (lessor) bushbaby (*Galago senegalensis*, E. Geoffroy 1796)	Arboreal, arboreal jumping	No. 18	M	Adult (25.7 cm)	USNM	US497310	o	o
Family Lemuridae								
Ring-tailed lemur (*Lemur catta*, Linnaeus 1758)	Arboreal/terrestrial	No. 19	M	Adult	PRI	PRI-Yoshikawa	o	o
		No. 20	F	Adult (43.3 cm)	USNM	US241365	o	o
Brown lemur (*Eulemur fulvus*, E. Geoffroy 1796)	Arboreal	No. 21	F	Adult (38.4 cm)	USNM	US502554	o	o
Ruffed lemur (*Varecia variegate*, Kerr 1792)	Arboreal	No. 22	M	Adult (51.2 cm)	PRI	KUPRI8439	o	o
Family Indridae								
Eastern avahi (*Avavi langer langer*, Gmelin 1788)	Arboreal, arboreal jumping	No. 23	F	Juvenile (15.2 cm)	AMNH	AMNH170500	o	o
Verreaux's sifaka (*Propithecus verreauxi*, A. Grandidier 1867)	Arboreal/terrestrial, terrestrial bipedal hopping	No. 24	F	Young (21.6 cm)	AMNH	AMNH170472	o	o
Family Lepilemuridae								
White-fotted weasel lemur (*Lepilemur mustelinus leucopus*)	Arboreal. arboreal jumping	No. 25	F	Sub-adult (21.8 cm)	MCZ	MCZ45418	o	o
Family Chirogaleidae								
Brown mouse lemur (*Microcebus rufus*, E. Geoffroy 1834)	Arboreal	No. 26	F	Adult (12.7 cm)	AMNH	AMNH174373	o	o
		No. 27	F	Adult (11.2 cm)	AMNH	AMNH174374	o	o
Total: 16 specimens								
Total		27 specimens						

Figure 2. Anatomical specialisations associated with the patagium and involved with the whole body and elongated neck in the Sunda colugo (*Galeopterus variegates*, **A–C**) and the number and body proportion in the Terrestrial treeshrew (*Tupaia tana*, **D**), slow loris (*Nycticebus coucang*, **E**), and ruffed lemur (*Varecia variegata*, **F**). Arrowheads indicate the coracohumerocutaneous muscle (fold) acting as a support system for the patagium; ProP — propatagium; PalatoP — palatopatagium; UroP — uropatagium; 1–7CV — first to seventh cervical vertebrae; 1–15TV — first to fifteenth thoracic vertebrae; 1–8LV — first to eighth lumbar vertebrae.

Furthermore, it was observed that the colugo neck was relatively longer to the body and thorax than in other mammals. Our used ratios of the relative lengths of total cervical vertebrae to total thoracic vertebrae (CVL/TVL) and to trunk body (CVL/BL), from thoracic to sacral vertebrae, were 0.817 and 0.717, respectively, in the Sunda colugo, and 0.397 and 0.427, respectively, in the Philippine colugo.

On the other hand, the ratios of CVL/TVL and CVL/BL are 0.268–0.475 (average: 0.357) and 0.122–0.211 (average: 0.163) in treeshrews, and 0.374–0.534 (average: 0.477) and 0.183–0.236 (average: 0.207) in strepsirrhines, respectively. A number of strepsirrhines (ring-tailed lemur, avahi, sifaka, and weasel lemur) show relatively longer CVL/TVL and CVL/BL ratios (0.524–0.623 and 0.208–0.247).

Therefore, these used ratios in colugos clearly show the elongated neck, as shown in elongated neck muscles like the sternomastoideus, cleidomastoideus, and infrahyoid.

Morphology of the cervicobrachial plexus

Colugo. All four aspects of the cervicobrachial plexus comprise the hypoglossal (*N. XII*) and the first cervical (C1) to second thoracic (T2) nerves; specifically, all cervical plexuses comprise *N. XII* and C1–C5, whereas all brachial plexuses comprise C6–T2 (Figs. 3, 4).

Among the sensory branches of the cervical plexus, the great auricular (GA) nerve, cranial (superior, TCS) and caudal (inferior, TCI) branches of the transverse cervical nerve, and several supraclavicular nerves (SCV, SCM, SCD) were easily recognised, although the lesser occipital nerve was not found in all specimens. All GAs were derived from C1 + 2. TCSs were derived from C1–C2 on three sides and from C1–C3 on one, thus forming a superficial cervical ansa with the cervical branch of the facial nerve (*N. VII*) and distributing their motor components to the platysma muscle and their sensory component to the skin. TCIs were derived from only C3 on three sides, while that on the fourth side received a communication branch from *N. VII* and C1–C2. SCs were derived from C4–C5 on all sides and were distributed to the ventrocaudal cervical area, which is a transitional area between the cervical, trunk, upper limb, and dorsal neck areas. On the other hand, the muscular branches of the cervical plexus tended to be delicate because their size was relative to muscular size. The cervical ansa, comprising *N. XII* and the ventral layers of C1–C2, was prominent and innervated the elongated infrahyoid muscles on all sides. The branches to the sternomastoid and cleidomastoid muscles, which derived from the accessory nerve (*N. XI*) and C1–C2, were extremely long because of the slender and elongated form of the muscle they supplied and the extended distance between them. The branches to the trapezius muscle were derived from *N. XI* and C4.

All brachial plexuses comprised the nerves C6–T2, which in turn formed two trunks: cranial (C6–C7) and caudal (C8–T2). All axillary arteries penetrated these trunks.

The ventral layers of these trunks formed a median ansa and then ramified into the musculocutaneous, median (M), and ulnar (U) nerves, whereas the dorsal layers formed one thick nerve bundle: the radial nerve (R). Moreover, the cranial and dorsal portions of the cranial trunk contributed to the suprascapular nerve and the subscapular and axillary nerves, respectively.

In the proximal area of the brachial plexuses, the pectoral nerves branched from the ventral layers of two trunks, forming the pectoral ansa, and inner-

Table 2. Number and length of vertebrae

Species*	Specimen no.	ID	Cervical vertebrae (CV)	Thoracic vertebrae (TV)	Lumbar vertebrae (LV)	Sacral vertebrae (SV)	Thoraco-lumbar vertebrae (TV+LV)	CVs length (CL)	Body length (BL) (TVs+LVs+SVs)	CVL/BL	TVs length (TVL)	CVL/TVL
(1) Colugo												
Family Cynocephalidae												
Sunda calugo (*Galeopterus variegatus*)	No. 1	US317290	7	13	6	5	19	3.19 cm	8.03 cm	0.397	4.45 cm	0.717
Philippina cotugo (*Cynocephalus volans*)	No. 2	US458984	7	13	6	4	19	3.88 cm	9.08 cm	0.427	4.75 cm	0.817
	No. 3	FM56532	NA									
	No. 4	FM56510	NA									
Total: 4 specimens										Ave. 0412		Ave. 0.767
(2) Treeshrew												
Family Tupaiidae												
Common treeshrew (*Tupaia glis*)	No. 5	Thor. 1963-1	7	13	6	3	19	0.98 cm	7.39 cm	0.133	3.27 cm	0.299
	No. 6	Thor. 1963-2	7	13	6	3	19	1.54 cm	9.66 cm	0.159	4.58 cm	0.336
	No. 7	US-A2173	7	13	6	3	19	1.27 cm	10.43 cm	0.122	4.73 cm	0.268
Terrestrial treeshrew (*Tupaia tana paitana*)	No. 8	US548343	7	13	6	3	19	2.24 cm	11.75 cm	0.191	5.48 cm	0.409
	No. 9	US39662	7	13	6	3	19	2.42 cm	11.45 cm	0.211	5.10 cm	0.475
	No. 10	US582439	NA									
Philippine treeshrew (*Urogala everetti*)	No. 11	FM61406	NA									
Total: 7 specimens										Ave. 0.163		Ave. 0.357
(3) Strepsirhini												
Family Lorisidae (Gray, 1821)												
Slow loris (*Nycticebus coucang*, Boddaert 1785)	No. 12	NA	7	16	7	?	23	NA	18.02 cm	0.183	8.10 cm	0.407
	No. 13	US502559	7	15	8	5	23	3.30 cm	20.74 cm	0.192	11.39 cm	0.350
Potto (*Perodicticus potto*, Muller 1766)	No. 14	US502567	7	16	6	6	22	3.99 cm				
Family Galagidae (Gray, 1825)												
Brown greater galago (*Otolemur crassicaudatus*, E. Geoffroy 1812)	No. 15	US502569	7	13	7	?	21	NA				
Northern (small-eared) greater galago (*Otolemur gametti pangariensis*, Ogilby 1838)	No. 16	US540881	7	14	6	3	20	1.32 cm	6.61 cm	0.194	3.53 cm	0.374
	No. 17	US540885	7	14	6	3	20	1.57 cm	7.61 cm	0.206	3.81 cm	0.412
Senegal (lessor) bushbaby (*Galago senegalensis*, E. Geoffroy 1796)	No. 18	US497310	7	14	6	3	20	3.55 cm	15.54 cm	0.228	7.23 cm	0.491
Family Lemuridae												
Ring-tailed lemur (*Lemur catta*, Linnaeus 1758)	No. 19	PRI-Yoshikawa	7	12	7	?	19	NA	23.09 cm	0.236	10.41 cm	0.524
Brown lemur (*Eulemur fulvus*, E. Geoffroy 1796)	No. 20	US241365	7	12	7	3	19	5.45 cm	22.62 cm	0.204	0.15 cm	0.504
	No. 21	US502554	7	12	7	3	19	4.62 cm	32.89 cm	0.205	14.58 cm	0.463
Ruffed lemur (*Varecia variegate*, Kerr 1792)	No. 22	KUPRI8439	7	12	7	3	19	6.75 cm				
Family Indridae												
Eastern avahi (*Avavi langer langer*, Gmelin 1788)	No. 23	AMNH170500	7	12	9	5	21	2.25 cm	9.15 cm	0.247	3.61 cm	0.623
Verreaux's sifaka (*Propithecus verreauxi*, A. Grandidier 1867)	No. 24	AMNH170472	7	11	8	4	20	2.99 cm	12.40 cm	0.241	4.9 cm	0.61
Family Lepilemuridae												
White-footed weasel lemur (*Lepilemur mustelinus leucopus*)	No. 25	MCZ45418	7	12	9	3	21	2.90 cm	13.95 cm	0.208	4.97 cm	0.584
Family Chirogaleidae												
Brown mouse lemur (*Microcebus rufus*, E. Geoffroy 1834)	No. 26	AMNH174373	7	13	7	?	20	1.42 cm	7.77 cm	0.183	3.29 cm	0.432
	No. 27	AMNH174374	7	13	7	?	20	1.14 cm	6.75 cm	0.169	2.64 cm	0.432
Total: 16 specimens										Ave. 0.207		Ave. 0.477
Total	27 specimens											

*The classifications were done from Groves (2005)

**Institution: AMNH — American Museum of Natural History, NY, USA; DMU — Anatomy Department, Dokkyo Medical University, Tochigi, Japan; FMNH — Field Museum of Natural History, IL, USA; MCZ — Museum of Comparative Zoology, Harvard University, MA, USA; PRI — Primate Research Institute, Kyoto University, Aichi, Japan; USNM — National Museum of Natural History, Smithsonian Institution, DC, USA
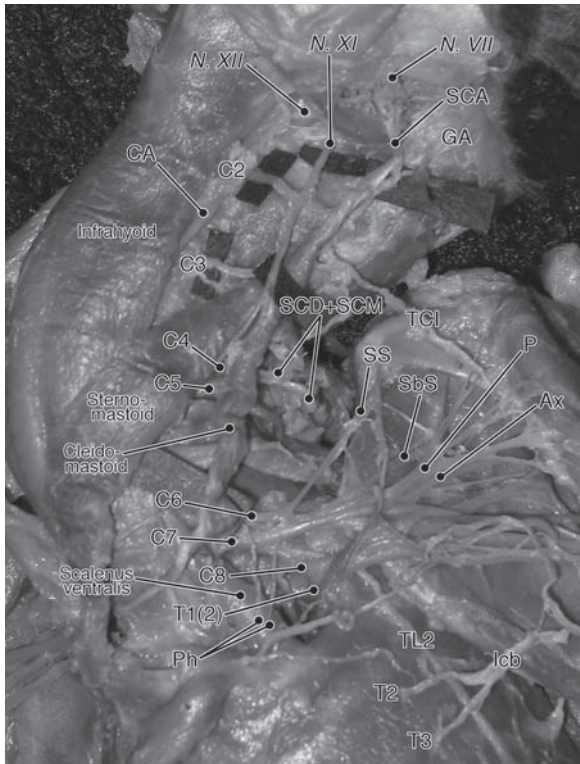
Figure 3. The composition of the cervicobrachial plexus in the Philippine colugo. The cervical plexus is composed of the hypoglossal (*N. XII*) and first cervical (C1) to fifth cervical (C5) nerves, whereas the brachial plexus is composed of the C6–T1(2); Ax — axillary nerve; CA — cervical ansa; C1–C8 — first to eighth cervical nerves; GA — great auricular nerve; Icb — intercostobrachial nerve; P — pectoral nerve; Ph — phrenic nerve; SbS — subscapular nerve; SCA — superficial cervical ansa; SCD — dorsal supraclavicular nerve; SCM — middle supraclavicular nerve; SS — suprascapular nerve; TCI — inferior transverse cervical nerve; TL2 — second long thoracic nerves; T1–T2 — first to second thoracic nerves; *N. VII* — facial nerve; *N. XI* — accessory nerve; *N. XII* — hypoglossal nerve.

1. Cervical plexus: *N. XII* + C1–C4, 12/12 sides (100.0%)
2. Brachial plexus: C5–T1, 7/12 sides (58.3%); C5–T2, 5/12 sides (41.7%)

On the other hand, the root segment of the cervicobrachial plexus in strepsirrhines showed anatomical diversity as follows (Figs. 5B, C).

1. Cervical plexus: *N. XII* + C1–C4, 27/32 sides (84.4%); *N. XII* + C1–C5, 5/32 sides (15.6%: right side of sifaka lemur and both sides of avahi and weasel lemur).
2. Brachial plexus: C5–T1, 11/32 sides (34.4%); C5–T2, 16/32 sides (50.0%); C6–T1, 1/32 sides (3.1%: sifaka-right side); C6–T1, 2/32 sides (6.3%: both sides of avahi); C6–T2, 2/32 sides (6.3%: both sides of weasel lemur).

Except for the absence of the lesser occipital nerve, the compositions of and branching points from the cervicobrachial plexus in treeshrews and strepsirrhines were almost common in their morphology with those in humans and most mammals: the GA, TCS, TCI, SCV, SCM, CA, Ph, SbC, P, MC, M, and U were derived from the ventral division, whereas the DS, SCD, SbS, Ax, R, and TD were derived from the dorsal divisions. Moreover, the scalenus ventralis muscle was absent in all treeshrews, whereas scalenus ventralis muscles were consistently observed in all strepsirrhines, as in humans and colugos.

DISCUSSION

Are the composition and branching pattern of the brachial plexus modified by functional (gliding) adaptations or evolutionary context?

Numerous functional morphological studies on forelimb osteology and myology in bats have been conducted to understand the unique locomotion of this exclusive flying mammal [45–47, 68–70]. According to Neuweiler [45], the relative length of the forelimb skeleton in the bat is unique for flying, although the wing comprises the same elements that comprise the mammalian forelimb. These include a large and strong humerus suspended from the scapula, an elongated forearm consisting of a thick and sturdy radius and a thin ulna, and elongated second to fifth metacarpals, which act as a support system for long but rigid spokes, like those of an umbrella. The same set of muscles that provide support for walking or running in four-legged animals serve as flight muscles in the bat, indicating that most forelimb muscles are common in mammals. However, all the power for wing movement is provided by strong chest and shoulder muscles, such as the pectoralis, subscapularis, and clavodeltoideus, although some muscles differ in position, length, and appearance [45, 46].
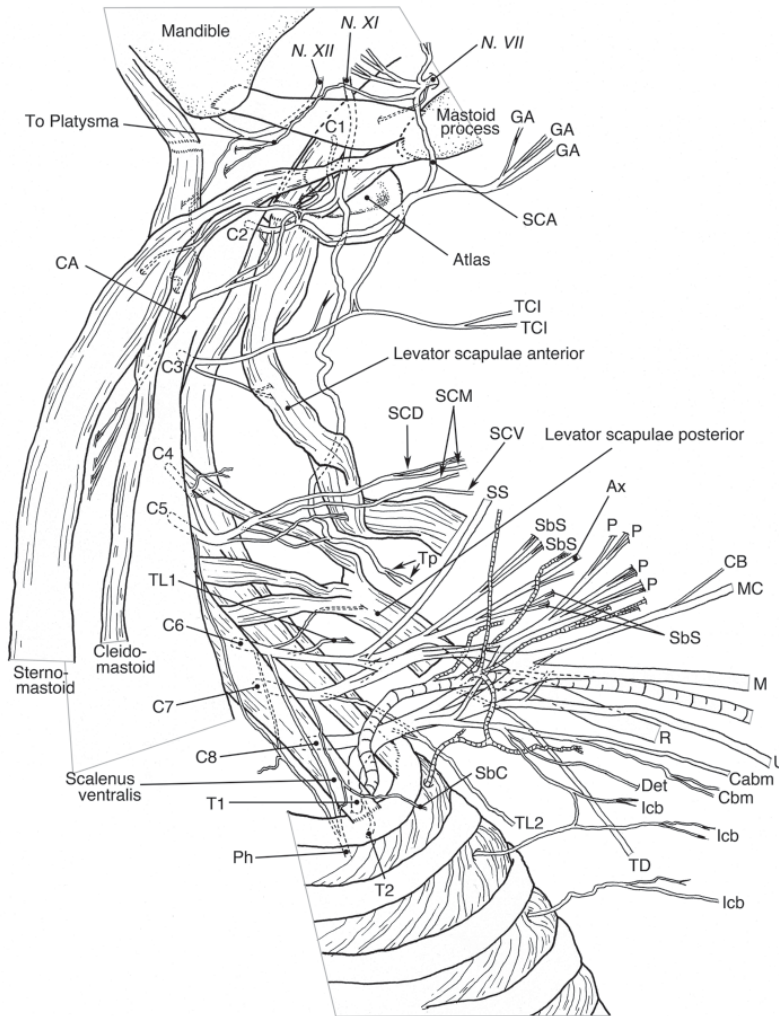
vated the major and minor pectoral muscles. The pectoral ansa and the branch to the dorsoepitrochlearis, medial antebrachial, and brachial cutaneous nerves tended to have a common origin at the proximal brachial plexus and communicated with the second and third intercostobrachial nerves.

In contrast, the long thoracic nerve innervating the anterior serratus muscle ramified from the dorsal layer of the proximal brachial plexus and divided into two nerves, the cranial (TL1) and caudal (TL2), which in turn ramified from the cranial and both trunks, respectively. The thoracodorsal nerve ramified from the dorsal layer of the posterior trunk or R.

Treeshrews and strepsirrhines. The root segment of the cervicobrachial plexus in treeshrews was extremely consistent, as follows (Fig. 5A).

Figure 4. The left brachial plexus in the Philippine colugo, *Cynocephalus volans* corresponding to Figure 3 (Case 1, FM56532); Ax — axillary nerve; CA — cervical ansa; Cabm — medial antebrachial cutaneous nerve; CB — nerve to coracobrachialis muscle; Cbm — medial brachial cutaneous nerve; C1–C8 — first to eighth cervical nerves; Det — nerve to dorsoepitrochlearis muscle; GA — great auricular nerve; Icb — intercostobrachial nerve; M — median nerve; MC — musculocutaneous nerve; P — pectoral nerve; Ph — phrenic nerve; R — radial nerve; SbC — subclavicular nerve; SbS — subscapular nerve; SCA — superficial cervical ansa; SCD — dorsal supraclavicular nerve; SCM — middle supraclavicular nerve; SCV — ventral supraclavicular nerve; SS — suprascapular nerve; TCI — inferior transverse cervical nerve; TCS — superior transverse cervical nerve; TD — thoracodorsal nerve; TL1–TL2 — first to second long thoracic nerves; Tp — nerve to trapezius muscle; T1–T2 — first to second thoracic nerves; U — ulnar nerve; *N. VII* — facial nerve; *N. XI* — accessory nerve; *N. XII* — hypoglossal nerve.

Thorington et al. [63–66] anatomically compared the forelimb bones, ligaments, and muscles of the flying squirrel (Pteromyinae) with those of the non-gliding (tree and ground) squirrel (Sciurinae) to elucidate their phylogenetic or functional significance. They discovered that in comparison with non-gliding squirrels, flying squirrels have (1) a longer forearm and shorter hand skeleton; (2) prominent articulations between the pisiform and scapholunate to provide a more stable base for the unique styliform cartilage supporting the wing tip; (3) prominent wrist ligaments for extreme gliding movements; (4) increased number of long muscles, such as the abductor pollicis longus, flexor carpi ulnaris, and palmaris longus, which are associated with extension and retraction of the styliform cartilage and wing tip of the plagiopatagium; and (5) several differences in forelimb musculature adapted for gliding movement. Therefore, not only the morphology of the somatic limb nervous system but also its relationship to

gliding locomotion remains unclear. In this study of colugos having unique gliding locomotion, the anatomical relationship between the cutaneous nerves to interdigital patagium and cervicobrachial plexus were uncertain because all dissected specimens were skinned. Moreover, the morphology of the cervicobrachial plexuses in treeshrews and strepsirrhines was not significantly shown in the relationship with their ecological habit or locomotion, such as terrestrial, arboreal, or gliding characteristics, in this study (Table 2). In the future, we will examine the relationship between the transformation of the cervicobrachial plexus and its ecological habit using extremely diversified mammals in detail.

Endo et al. [10] mentioned that the branching point between M and U is considered to be more distal in some mammals with elongated limbs, such as the giraffe and okapi, when compared with that in other ruminants. Owing to relatively longer forelimbs in the colugo, this branching point is very simi-
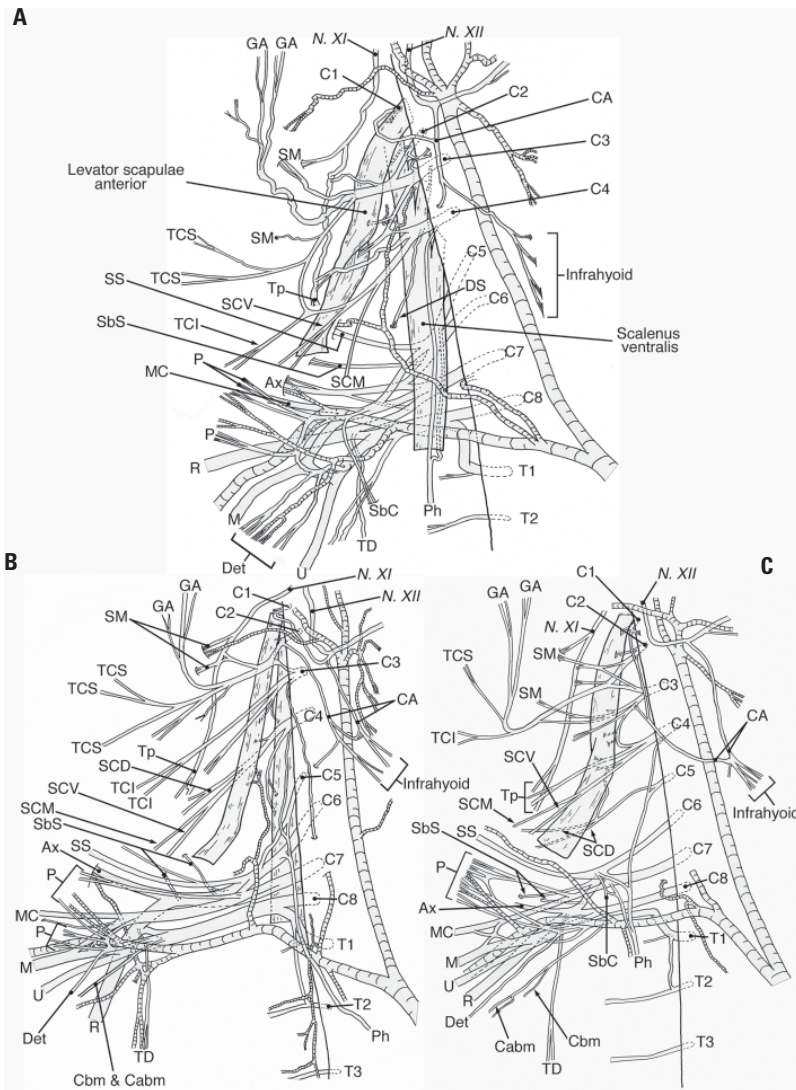
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Figure 5. The right brachial plexuses in the terrestrial treeshrew (*Tupaia tana*, **A**), slow loris (*Nycticebus coucang*, **B**), and weasel lemur (*Lepilemur mustelinus*, **C**); Ax — axillary nerve; CA — cervical ansa; Cabm — medial antebrachial cutaneous nerve; CB — coracobrachialis muscle; Cbm — medial brachial cutaneous nerve; C1–C8 — first to eighth cervical nerves; Det — nerve to dorsoepitrochlearis muscle; GA — great auricular nerve; Icb — intercostobrachial nerve; M — median nerve; MC — musculocutaneous nerve; P — pectoral nerve; Ph — phrenic nerve; R — radial nerve; SbS — subscapular nerve; SCA — superficial cervical ansa; SCD — dorsal supraclavicular nerve; SCM — middle supraclavicular nerve; SCV — ventral supraclavicular nerve; SS — suprascapular nerve; TCI — inferior transverse cervical nerve; TCS — superior transverse cervical nerve; TD — thoracodorsal nerve; TL1–TL2 — first to second long thoracic nerves; Tp — nerve to trapezius muscle; T1–T2 — first to second thoracic nerves; U — ulnar nerve; *N. VII* — facial nerve; *N. XI* — accessory nerve; *N. XII* — hypoglossal nerve.

lar to that in most mammals, and should be examined further in long-limbed mammals.

Leche [38] also described the brachial plexus in the colugo as forming a common trunk between M, U, and R in the axillary area and dividing them into a distal brachial part. In all the colugo specimens examined in this study, the branching pattern from the brachial plexus and the penetrating point of the axillary artery into the brachial plexus were almost identical to those found in our previous studies on primates, including humans [22–27, 75, 76].

These results suggest that it is problematic to correlate the transitional or continuous changes in the brachial plexus of placental mammals with any evolutionary context because the branching pattern, height, and position of the brachial plexus in the

colugo are almost identical to those in primates, including humans and most placental mammals such as domestic animals. In addition, it appears problematic to demonstrate any functional modification of brachial plexus morphology in gliding mammals, although the skeleton and muscles of the upper limb are somewhat specialised and the innervation to the cutaneous muscles and patagium are expected to be uniquely adapted for gliding and flying.

Functional changes in the cervicobrachial plexus of long-necked mammals

Over many years, the modification of *N. XI* in long-necked mammals has received considerable attention. Some authors described the lack of a normal *N. XI* in some long-necked mammals, such as the camel, llama, and giraffe, and how the trapezius and sterno-

cleidomastoid muscles in these mammals were innervated only by cervical nerves comprising the *N. XI* component after running within the spinal cord [18, 67, 71]. Although Zuckerman and Kiss [77] identified *N. XI* in the giraffe and concluded that it is unlikely to replace the *N. XI* component by another nerves, they finally accepted the absence of *N. XI* in the camel [29]. Because the normal, independent *N. XI* was observed in all specimens examined in our study and in long-necked specimens examined in previous studies, it appears that the absence of *N. XI* is not a constant finding in long-necked mammals, although this requires further examination.

Solounias [57] mentioned that C5, C6, and T2 do not contribute to the brachial plexus in the giraffe, whose brachial plexus is comparatively concentrated. Endo et al. [10] reported that C7, C8, and T1 were much thicker and formed the main components of the brachial plexus in the okapi, whereas C6 was the thinnest of all roots and C5 did not contribute at all.

The brachial plexus in the giraffe [72] and camel [50] reportedly comprises C6–T1, although such a concentrated brachial plexus has been reported in certain mammals, such as the porcupine, cat, gnu, and dog, irrespective of their neck length [42, 50]. Although it is true that C5 does not always contribute to the brachial plexus irrespective of neck length [42, 50], there is some positive correlation between an elongated neck and a concentrated brachial plexus based on current and previous reports.

Recently, Sekiya et al. [54] reported the specialised morphology of the brachial plexus in a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) in detail and it exhibited broader root segments composed of C3–T1 in this short-necked mammal.

On the other hand, any relationship between neck length and T2 (or the lowest contribution to the brachial plexus) is hard to establish because T2 has numerous anatomical variations as a contributor in every mammal, including humans. If T2 contributes to the brachial plexus, it includes only part of the ventral division; this contribution is not purely a somatic spinal nerve and is known as Kuntz's nerve because it always conveys sympathetic fibres from the stellate (cervicothoracic) ganglion to the forelimb [34, 49, 52]. Therefore, it is extremely difficult to argue in favour of a T2 somatic component as part of the brachial plexus, or a relationship between neck length and the lower limit of the brachial plexus.

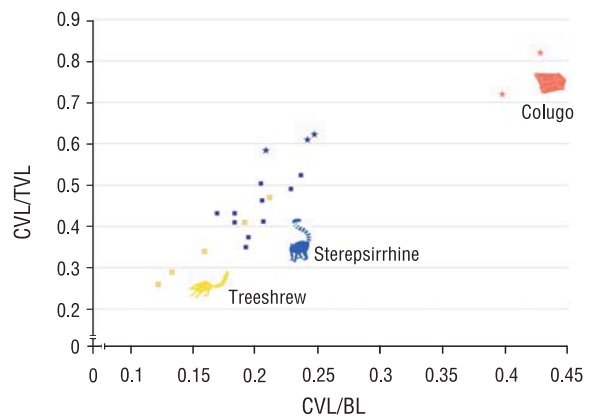In the present examination, the colugo with the broader cervical (*N. XII* and C1–5) and con-

Figure 6. The relationship between the relative cervical lengths (CVL/TVL, CVL/BL) and root segments of the cervicobrachial plexus. The stars show the broader cervical plexus composed of *N. XII* and C1–5 and concentrated brachial plexus composed of C6–T1(2), whereas the squares show widely-observed root segments of the cervical plexus composed of *N. XII* and C1–4 and brachial plexus composed of C5–T1(2) in most terrestrial placental mammals. These results clearly show that the semi-elongated species, which have higher CVL/TVL and CVL/BL ratios, reflect the broader cervical and concentrated brachial plexuses.

centrated brachial (C6–T1(2)) plexuses was a semi-elongated neck as shown in our ratios (CVL/BL 0.412; CVL/TVL 0.767), and three strepsirrhines, avahi, sifaka, and weasel lemur, with a similar root transformation of the cervicobrachial plexus were also relatively longer-necked (average: CVL/BL 0.232; CVL/TVL 0.606) than those in others, the averages of which in treeshrews were CVL/BL: 0.163 and CVL/TVL: 0.357, whereas the averages in strepsirrhines were CVL/BL: 0.207 and CVL/TVL: 0.477 (Table 2, Fig. 6).

CONCLUSIONS

Hence, our results suggest as follows:
1. Although the number and proportion of individual vertebrae vary, the ratios between CVL/TVL and CVL/BL are correlative as a marker of the relative cervical length.
2. The root segments of the broader cervical (*N. XII* +C1–5) and concentrated brachial (C6–T1(2)) plexuses in both colugos and certain strepsirrhines were relatively semi-elongated neck species as shown in our ratios: CVL/TVL and CVL/BL.

On the basis of the present and previous reports in long-necked mammals, the cranial components of the brachial plexus, such as C5 and C6, tend to be excluded from forelimb innervation, and their distribution is rather to the lower neck and its sur-
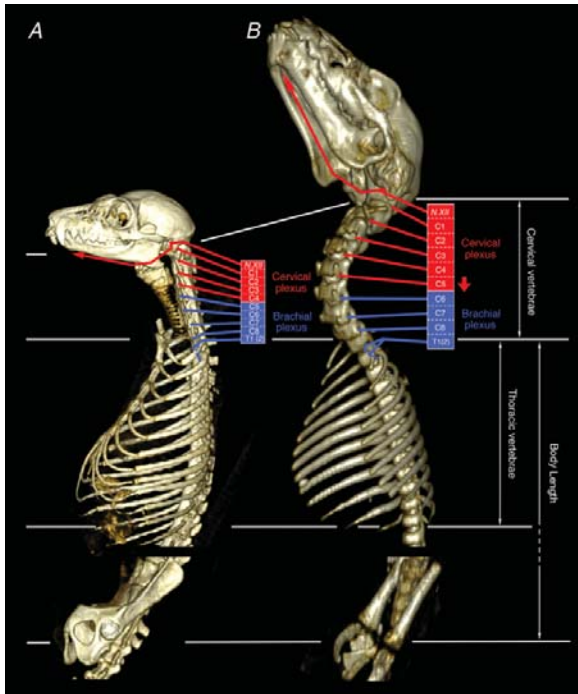
Figure 7. The transformation of the cervicobrachial plexus with the relationship of the relative cervical length; **A.** Brown lemur, showing the general morphology of primates, including humans; **B.** Colugo. Elongated cervical and concentrated brachial plexus roots are recognized along with cervical–thoracic vertebrae and body trunk.

rounding structures (Fig. 7). Therefore, the colugo's cervicobrachial plexus appears to relate more to neck length than to specialised locomotion or any phylogenetic or evolutionary constraint.

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