J. Anat. (1997) **190**, pp. 447–455, with 8 figures Printed in Great Britain

On the morphology of the brachial plexus of the platypus (*Ornithorhynchus anatinus*) and the echidna (*Tachyglossus aculeatus*)

MASAHIRO KOIZUMI* AND TATSUO SAKAI

Department of Anatomy, Juntendo University School of Medicine, Tokyo, Japan

(*Accepted 2 December 1996*)

ABSTRACT

Four forelimbs of 3 platypuses and 3 forelimbs of 2 echidnas were examined to study the precise form of the brachial plexus and to clarify the structural characteristics of the brachial plexus in phylogeny. The spinal components contributing to the plexus (C4–T2) and the formation patterns of the 3 trunks of the plexus were the same as those generally observed in mammals. In the cranial half of the brachial plexus from C4, 5 and 6 in monotremes, division into the ventral bundle (lateral cord) and dorsal bundle (axillary nerve) is clear, as in other mammals. However, for monotremes, in the caudal half of the plexus from C7 and T1 (+T2) and the nerves arising from the caudal plexus there is no definite division into the ventral and dorsal bundles, which distribute to the flexor and extensor parts of the forelimbs, respectively. The lower trunk of the monotreme brachial plexus forms a cord which contains both ventral and dorsal components. This characteristic diverges from the generally accepted idea that the tetrapod limb plexus is divided clearly into 2 layers: a dorsal layer for extensors and a ventral layer for flexors of the limb. Considering the incomplete dorsoventral division of forelimb nerves in some reptiles and urodeles, the caudal half of the monotreme brachial plexus has characteristics in common with those of lower tetrapods.

Key words: Monotremes; peripheral nervous system.

INTRODUCTION

The importance of the upper limbs in human life is very evident and the nerves distributed to the upper limbs are of considerable medical and surgical importance. The practical treatment of upper limb nerve injury such as brachial plexus trauma requires appropriate knowledge about segmental motor innervation and the precise course of individual nerves. Many clinical studies have been undertaken using electrical stimulation of exposed nerves during operation and electromyography to record the muscles activated (Brodal, 1969; Dyck et al. 1988).

Some anatomical studies have reported that ramification of the upper limb nerves has a regular pattern (Yamada, 1986; Homma & Sakai, 1991). The complexity of the brachial plexus has attracted many observers. To clarify the basic structure of its complex pattern, many anatomists have traced nerve bundles and have studied its segmental components (Schumacher, 1908; Kerr, 1918; Chiba, 1984) or the branching patterns (Kodama et al. 1987; Koizumi, 1989; Koizumi & Sakai, 1995) of the plexus. Additionally, the stratified structure of the plexus has been reported to have a close relationship with the dorsoventral arrangement of limb muscles (Bolk, 1902; Kato & Sato, 1984) and the fundamental pattern of the plexus strata has been studied.

By observing the brachial plexuses of monotremes (platypus and echidna), we have obtained informative new results concerning the phylogeny of the brachial plexus. Monotremes are known to be unique mammals and to display reptile-like characteristics. Although the brachial plexus of monotremes has also been examined by other authors (Westling, 1889; Manners-Smith, 1894; McKay, 1894; Howell, 1937), the stratified structure of the brachial plexus has not been discussed. The purpose of this study is to

---

Correspondence to Dr M. Koizumi, Department of Anatomy, Juntendo University School of Medicine, 2-1-1 Hongo, Bunkyo-ku, Tokyo 113, Japan.

* Present address: Department of Anatomy, Kumamoto University School of Medicine, 2-2-1 Honjo, Kumamoto, 860 Japan.

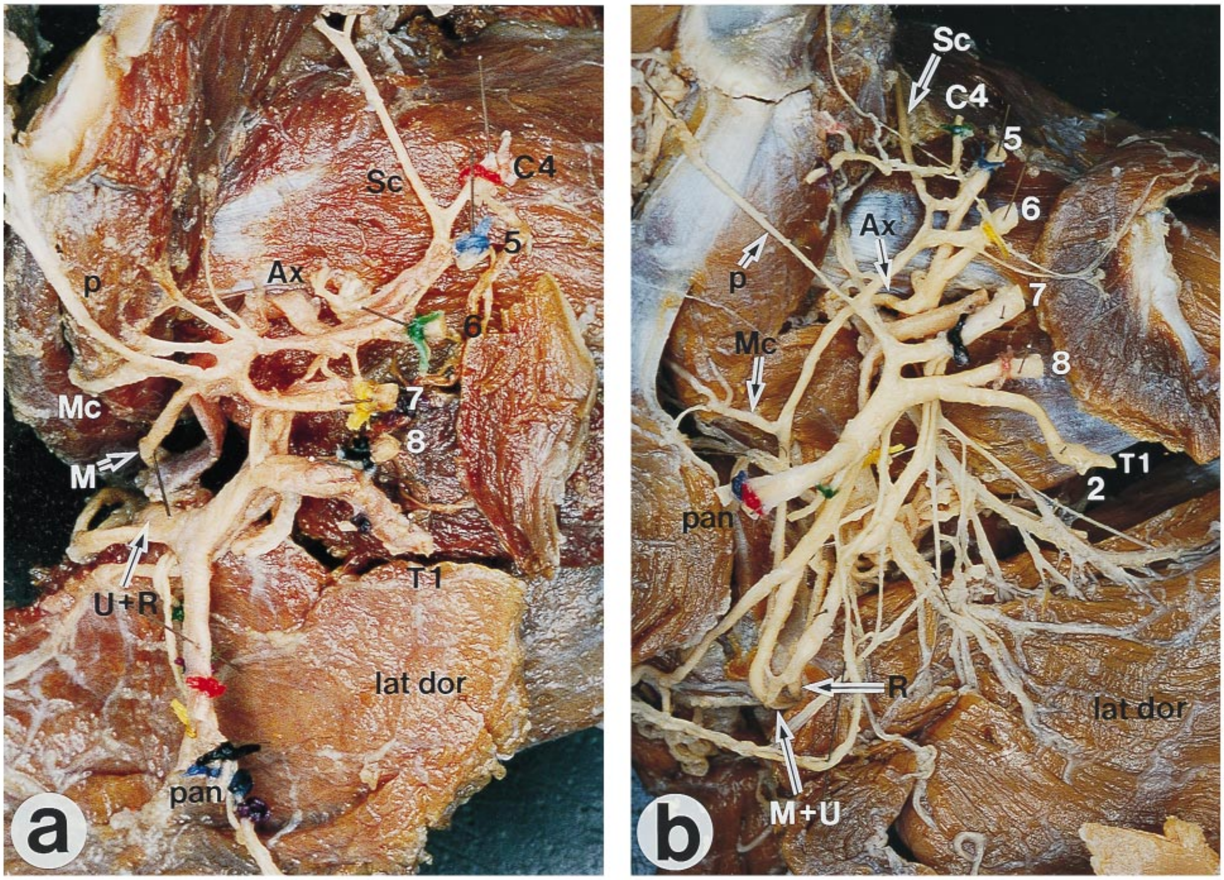

Fig. 1. Two examples of a brachial plexus: (*a*) in the right forelimb of a platypus (UQ102d) and (*b*) in the right forelimb of an echidna (UQ002d). Ax, axillary nerve; Axl, axillary artery; cbr, nerve to coracobrachialis muscle; C3–8, 3rd–8th cervical nerves; Fc, caudal cord (caudal fascicle); Fl, lateral cord (lateral fascicle); Intercost, intercostal nerve; lat dor, latissimus dorsi muscle; M, median nerve; Mc, musculocutaneous nerve; p, nerve to pectoralis muscle; pan, panniculus carnosus muscle; pect, pectoral muscle; Phr, phrenic nerve; R, radial nerve; Sc, supracoracoid nerve; subscap, subscapularis muscle; suprasp, supraspinatus muscle; st-epc+cost-cor, sternoepicoracoid and costocoracoid muscles; ter maj, teres major muscle; ter min, teres minor muscle; T 1–2: 1st–2nd thoracic nerves; Ti, lower (inferior) trunk; Tm, middle trunk; Ts, superior (upper) trunk; U, ulnar nerve.

elucidate the morphological characteristics of the brachial plexus in monotremes, and to discuss its stratified structure.

MATERIALS AND METHODS

Four forelimbs from 3 platypuses (*Ornithorhynchus anatinus*) and 3 from 2 echidnas (*Tachyglossus aculeatus*) were examined. All 3 platypuses were female and both echidnas were believed to be female. All specimens were from the Department of Zoology, University of Queensland, Australia, where they were preserved in a frozen state. After thawing, the specimens were fixed initially by formalin (10%) and alcohol (50%) later. The observations were obtained as follows. After peeling off the skin, the specimens were dissected to expose the brachial plexus. Each spinal root contributing to the plexus, the axillary artery/vein, and the muscles surrounding the shoulder region were separated from the body. The nerve fibre composition of the plexuses of the arm specimens were carefully observed under a stereomicroscope after stripping off the epineurium, and the perineurium if necessary.

RESULTS

Spinal segments contributing to the brachial plexus

The brachial plexuses of the monotremes observed in the present study were formed by the ventral rami of the lower 5 cervical nerves (C4–8) and the 1st thoracic nerve (T1). In forelimbs of 2 platypuses (specimen nos 101s, 102s) and both forelimbs of an echidna (002d,s), a fine branch from the ventral ramus of the 2nd thoracic nerve (T2) also joined the plexus (Figs 1, 2, 4). Observation by tracing nerve fascicles established that C4 constituted not only the phrenic nerve and the branches to the sternoepicoracoid and costocoracoid muscles, but also the supracoracoid

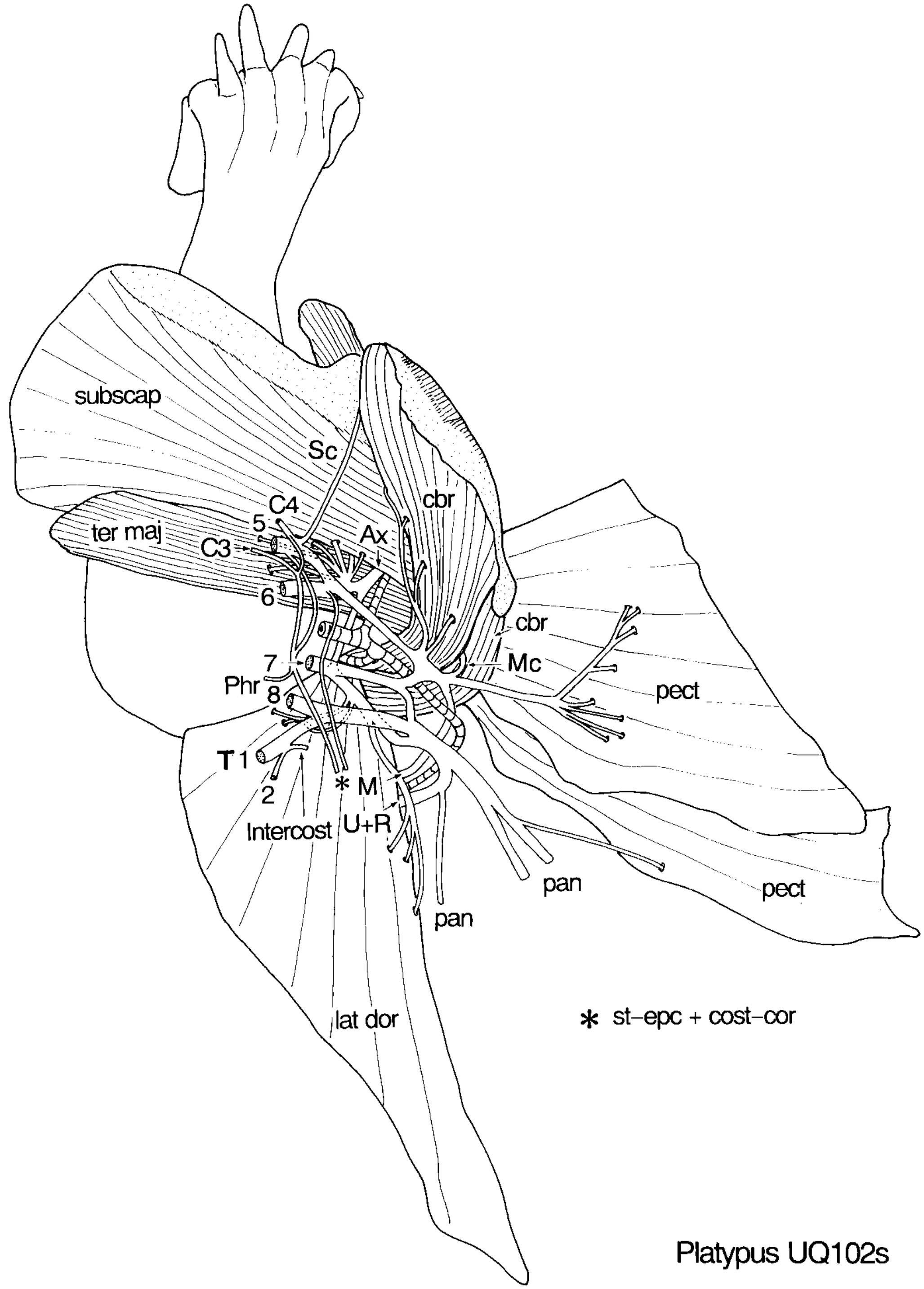

Fig. 2. Drawing of the brachial plexus and shoulder muscles in the left forelimb of a platypus seen from the anteromedial aspect. Each spinal root contributing to the plexus, the axillary artery and the origins of the pectoral and latissimus dorsi muscles are separated from the body. Note that the ulnar and radial nerves are not divided in the upper forelimb region. For abbreviations, see Figure 1.

and axillary nerves. The nerve fibres from T2 were confirmed to join the plexus together with T1. The 3rd cervical nerve (C3) did not contribute to the plexus, but only to the phrenic nerve and the branches to the sternoepicoracoid and costocoracoid muscles. In one forelimb of an echidna (001d), a fine communicating branch between the roots of C3 and C5 was observed. The distribution of nerve fibres in this communication was not established.

Construction of the brachial plexus

In the brachial plexus of the platypus, 3 trunks were identified, as in man (Figs 1–3). C4 and 5 joined just

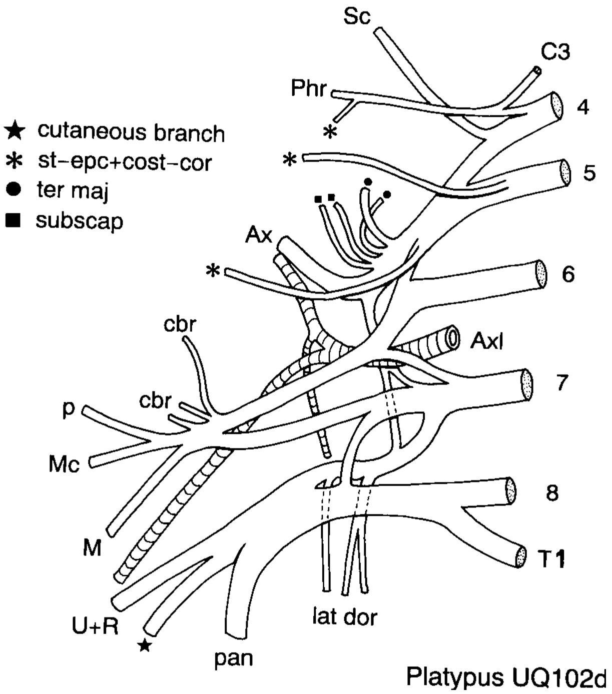

Fig. 3. Illustration of the brachial plexus in the right forelimb of the same platypus as in Figure 1*a*. T2 does not join the plexus in this case. The caudal cord formed by C7 + 8 + T1 contains both ventral (ulner nerve) and dorsal (radial nerve) nerve components. For abbreviations, see Figure 1.

after they emerged from the intervertebral foramina to form the common stem. Distally, this common stem and C6 formed an upper trunk, which was very short as it split into dorsal and ventral divisions immediately after formation. The middle trunk comprised only C7. The lower trunk comprised C8 together with T1 (+2).

In both forelimbs of one echidna (002d,s) (Fig. 4), on the hand, the common stem of C4 + 5 and the stem of C6 were separated into dorsal and ventral divisions. The dorsal and ventral divisions of both stems joined to form the dorsal and ventral common cords, respectively. These common cords, together, can be termed the upper trunk, although an upper trunk was, strictly speaking, not found in these cases. The other echidna (001d) (Fig. 5) had the same upper trunk form as that in the platypus.

Although the formation of the upper trunk differed in appearance between the platypus and the echidna, analysis by stripping off the epineurium revealed that the pattern of the dorsoventral division of the upper trunk in the platypus was similar to that of the echidna (Figs 6, 7). In both species, the common stem of C4 + 5 and the stem of C6 formed common ventral and dorsal cords after splitting into dorsal and ventral divisions.

The dorsal division of the upper trunk (C4 + 5 + 6) in all cases passed in a dorsal direction between the subscapular and teres major muscles, giving off branches to both muscles and then forming the axillary nerve (Figs 2, 4). The axillary nerve supplied the deltoid and teres minor muscles and the dorsal surface of the upper limb. Before passing between those 2 muscles, a fine communicating twig between the dorsal division of the upper trunk (axillary nerve) and the middle trunk was observed dorsal to the axillary artery (◎ in Figs 6, 7). This branch is further mentioned later.

The middle trunk divided into several branches. One was the communicating branch with the axillary nerve. Secondly, a ventral branch of the middle trunk joined the ventral cord of the upper trunk to form the lateral cord. The remaining 2 (platypus 101s, 102d,s; echidna 002d) or single (platypus 103s; echidna 001d, 002s) branch(es) from the middle trunk joined the lower trunk. Fascicular tracing analysis showed that the branch from the middle trunk to the lower trunk contained 2 kinds of cords; one was from the ventral side of the middle trunk (v-type branch; ⓥ in Figs 6, 7) and the other from the dorsal side (d-type branch; ⓓ in Figs 6, 7). The v-type branch carried many nerve fibres to the panniculus carnosus muscle. Some fibres in the v-type branch were included in the nerves to the forelimb. The d-type branch, arising from the lower trunk in a single branch or several bundles, had no relation with the panniculus carnosus. After giving off nerves to the latissimus dorsi, the d-type branch communicated with a branch from the lower trunk to form the radial and ulnar nerves.

In the connecting branch between the middle trunk and the axillary nerve (mentioned above; ◎ in Figs 6, 7), 2 streams of nerve fibres were observed. One ran from the middle trunk to the axillary nerve and the other from the axillary nerve to the d-type branch mentioned above.

The lower trunk formed a caudal cord receiving the branches from the middle trunk. In the platypus (Fig. 6), the caudal cord divided into the ulnar and radial nerves near the medial epicondyle of the humerus. The median nerve mainly originated from the lateral cord. Near the elbow, a fine communicating branch was observed running from the ulnar nerve to the median nerve. This branch contained the fibres from C8 to T1(+2). A further analysis of nerve fascicles revealed that the fibres of the ulnar and radial nerves were intimately mingled during the course in the upper arm. We could not separate one from the other.

In the echidna (Fig. 7) some branches from the caudal cord ran along the medial side of the upper arm and exchanged fibres with each other. At the distal part of the upper arm, they formed 2 main

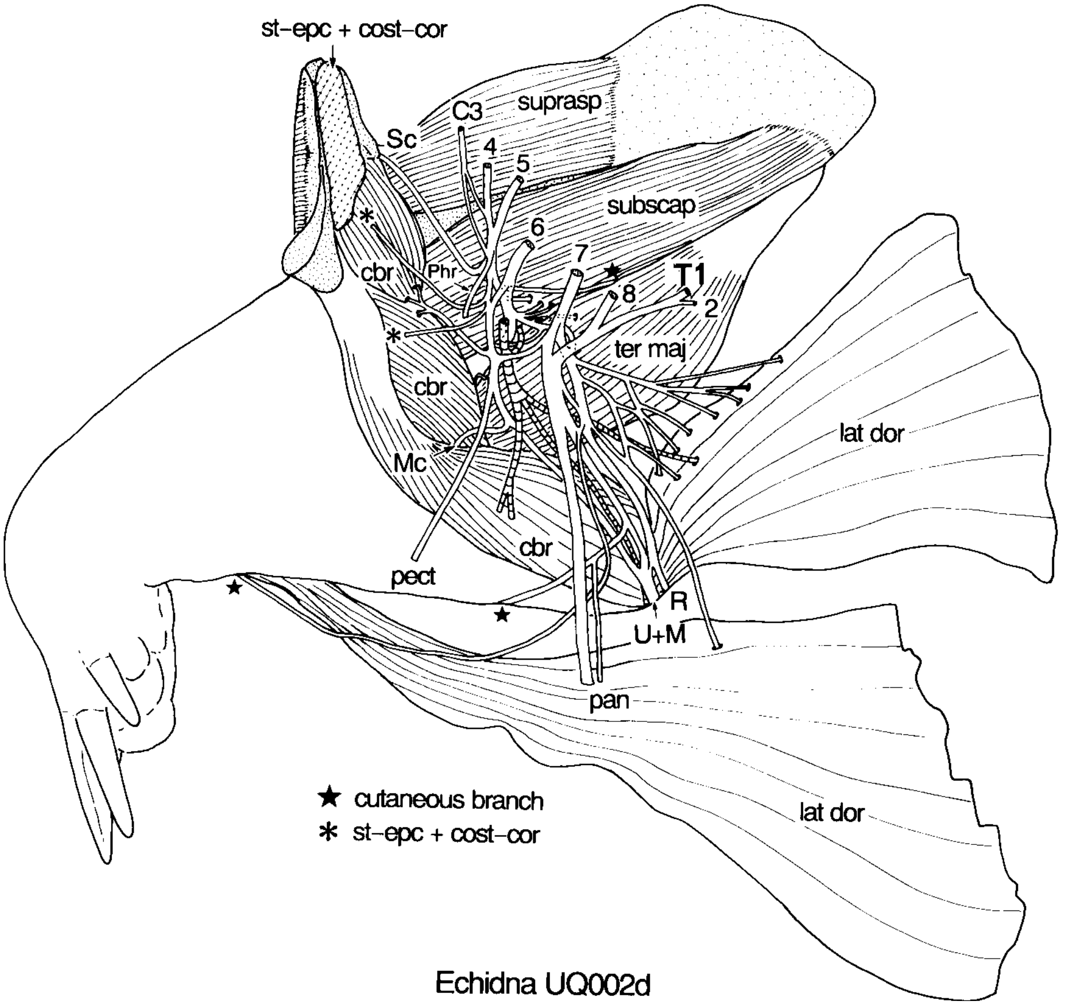

Fig. 4. Drawing of the brachial plexus and shoulder muscles in the right arm of the same echidna as in Figure 1*b*. The insertion of the sternoepicoracoid and costocoracoid muscles are indicated in the latticed area. The formation pattern of the median, ulnar and radial nerves is different from that of the platypus. At the distal end of the forelimb, the radial nerve can be distinguished from the common stem of the median and ulnar nerves. The median and ulnar nerves can be identified a little more distally. For abbreviations, see Figure 1.

branches. One was the radial nerve. The other branch gave off the cutaneous and muscular branches to the panniculus carnosus and joined the lateral cord to form a bundle, which bifurcated into the median and ulnar nerves. In all echidna limbs, the ulnar nerve received a fine communication from the radial nerve at the elbow. A tracing analysis of nerve fascicles revealed that each of the median and ulnar nerves had nerve fibres from both the lateral and caudal cords.

DISCUSSION

Characteristics of the brachial plexus in monotremes

The brachial plexuses of monotremes are shown schematically in Figure 8. The constant contribution of C4 to T1, and the frequent contribution of T2 into the plexus indicate that the range of segmental components of the plexus in monotremes is within the variation of that in mammals generally (Miller, 1934; Harris, 1939). This agrees with the descriptions of previous studies (Westling, 1889; Manners-Smith, 1894; McKay, 1894; Miller, 1934; Howell, 1937; Harris, 1939). With respect to the formation patterns of the upper, middle and lower trunks of the plexus, there are no essential differences between monotremes and man.

The most conspicuous characteristic of the brachial plexuses of monotremes is that there is an obvious difference in the formation patterns of the cords between the cranial and caudal segments of the plexus. In the cranial half of the brachial plexus from C4+5+6 in monotremes, division into ventral and dorsal bundles is clear, as in mammals generally. In monotremes, the ventral bundle made by a union of the ventral divisions of the upper and middle trunks gives rise to the musculocutaneous and median nerves, and is homologous with the lateral cord in the

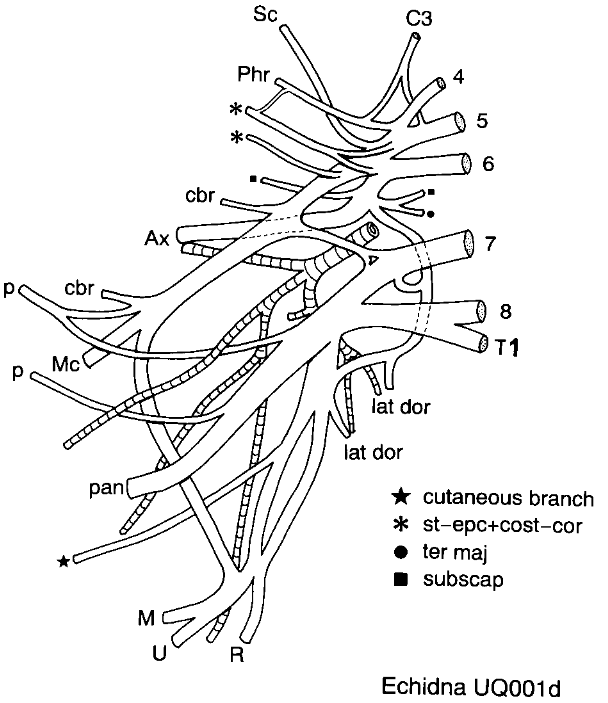

Fig. 5. Illustration of the brachial plexus in the right arm of another echidna. T2 does not join the plexus in this case. For abbreviations, see Figure 1.

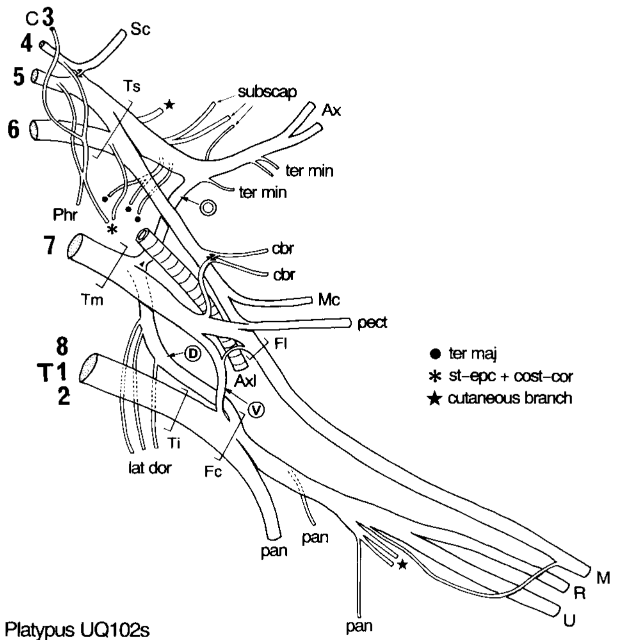

Fig. 6. Fascicle tracing analysis of the brachial plexus and its nerves for the same specimen as shown in Figure 2. Ventral view in the region of the axilla and upper forelimb to the elbow. In the upper forelimb, the nerve fibres of the ulnar and radial nerves are intimately mingled, even after the removal of the epineurium. The nerve bundles marked with Ⓓ, Ⓥ and ◎ are mentioned in the text. For abbreviations, see Figure 1.

brachial plexus of humans. The dorsal bundle, made by the dorsal divisions of the upper and middle trunks, forms the axillary nerve.

On the other hand, in the caudal half of the plexus from C7+8+T1(+2) in monotremes, there is no definite division into the ventral and dorsal bundles which distribute to the flexor and extensor parts of the upper limbs, respectively. In other words, the lower trunk of the monotreme brachial plexus has no definite division into ventral and dorsal bundles, and forms a cord containing both ventral and dorsal components. Howell (1937) described this cord as caudal mixed cords. The medial and posterior cords observed in man are not found in monotremes.

Miller (1934) found that the bundle derived from the lower trunk of the brachial plexus in monotremes had no dorsal (extensor) components. However, his identification of the peripheral nerves from the plexus was incorrect because he confused the axillary nerve with the radial nerve. The present observation clearly shows that the bundle from the lower trunk of the plexus in monotremes contains both ventral and dorsal components of nerve fibres, and gave off the branches to the panniculus carnosus muscle, and ulnar and radial nerves.

Furthermore, in monotremes, the nerves originating from the caudal cord exchange nerve fascicles with each other until reaching the elbow. In the platypus, after the removal of epineurium, the fibres of the ulnar (for flexors) and radial (for extensors) nerves are mingled intimately until reaching the distal end of the upper arm, where the 2 nerves are obviously distinguished. This fact means that isolation of the radial nerve from the flexor nerves already in the proximal part of the upper arm, as observed in man, is not a constant occurrence in phylogeny. It should be noted that, in monotremes, the radial nerve takes a different course in the upper arm than in man, running along the medial side of the upper arm together with the median and ulnar nerves.

Dorsoventral division of the brachial plexus in tetrapods

Are the forelimb nerves in tetrapods arranged dorsoventrally in a stratified pattern in the brachial plexus? This problem has been studied since the last century. Fürbringer identified 4 layers in the brachial plexus (Gaupp, 1899) and Bolk (1902) identified 5 layers. Some recent authors have traced nerve fascicles in the plexus and clarified the stratified relationship among each forelimb nerve (Kodama et al. 1987; Koizumi, 1989; Koizumi & Sakai, 1995). Most textbooks of human anatomy indicate the dorsoventral division as 2 layers instead of more at the proximal part of the

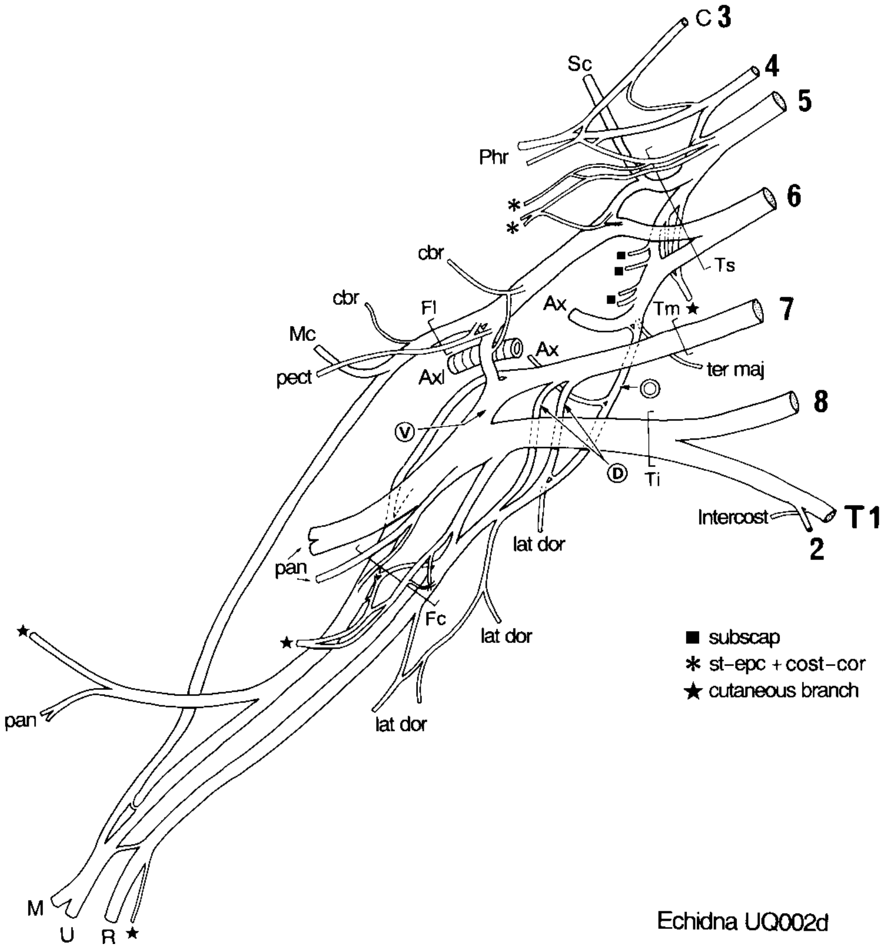

Fig. 7. Fascicle tracing analysis of the brachial plexus and its nerves for the same specimen as shown in Figure 4. Ventral view in the region of the axilla and upper forelimb to the elbow. In the upper forelimb the median, ulnar and radial nerves exchange nerve fibres with each other. The nerve bundles marked with Ⓓ, Ⓥ and ◎ are mentioned in the text. For abbreviations, see Figure 1.

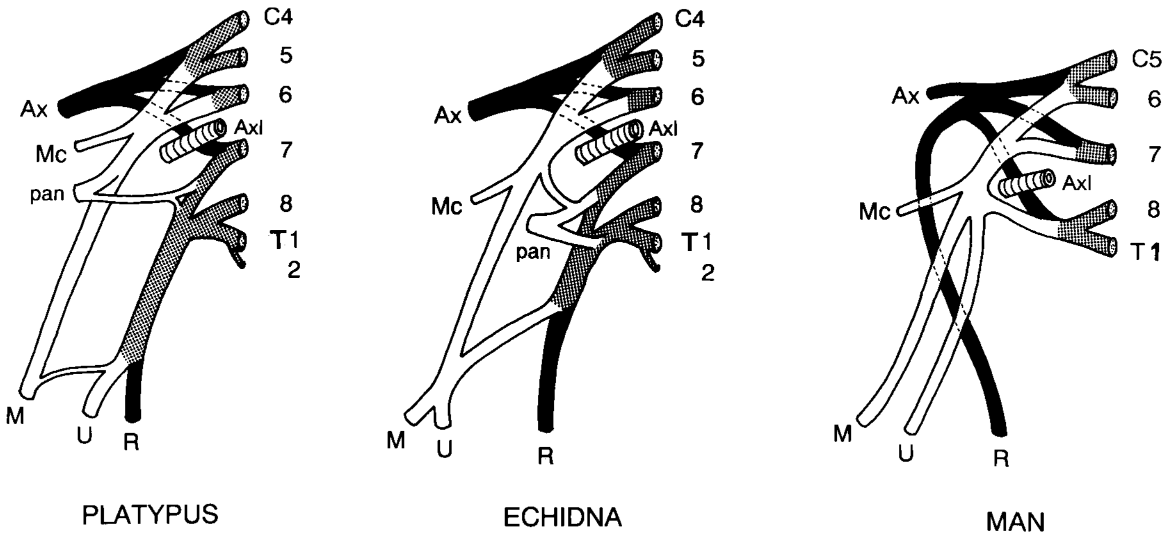

Fig. 8. Schematic diagrams showing the formation patterns of the brachial plexus and its main nerves from the root of each spinal component to the elbow. Ventral view. Of the plexus and nerves, dorsal (extensor) components are shown in black, ventral (flexor) in white, and mixed components in grey. In man, the upper, middle and lower trunks of the brachial plexus are divided dorsoventrally into 2 layers. However, in monotremes (2 examples at left), the dorsoventral division does not occur in the caudal half of the plexus until reaching the distal upper forelimb, where an extensor nerve (radial nerve) is obviously identified. For abbreviations, see Figure 1.

brachial plexus (Schaeffer, 1953; Woodburne & Burkel, 1988; Williams et al. 1985). The division of tetrapod limb plexus into a dorsal layer for the extensor muscles and a ventral layer for the flexor muscles has been generally accepted as a basic pattern in phylogeny (Paterson, 1887; Ballard, 1964; Starck, 1982). The present study reveals that monotremes keep this basic feature of tetrapods in the cranial half of the brachial plexus. In this point, our findings support the generally accepted idea about the dorsoventral division of the plexus.

On the other hand, the findings observed in the caudal half of the monotreme brachial plexus arouse doubt about the generally accepted idea of dorsoventral division. The analysis by tracing nerve fascicles in the plexus reveals that the dorsal and ventral nerve components cannot be separated from each other in the caudal cords, and that they are mixed intimately in the common epineurium. Further, Straus (1941) and Haines (1939) reported findings showing that the dorsoventral division of the limb plexus was not complete in primitive tetrapods. According to them, some extensor antebrachial muscles were supplied by the flexor nerve in some urodeles and some reptiles. Harris (1939) illustrated the brachial plexuses of urodeles and some reptiles, in which the dorsoventral division was obscure. These facts suggest that incomplete dorsoventral (extensor–flexor) division of the forelimb nerves occurs not only in the caudal half of the plexus of monotremes, but is also commonly observed in lower tetrapods.

The present findings indicated that the brachial plexuses of monotremes have 2 different features. Those are the mammal-like feature in the cranial half, and the feature common to lower tetrapods in the caudal half. Recently, the limb posture and locomotor patterns of monotremes are reported to have features characteristic of the locomotively generalised therians (Jenkins, 1970; Prodmore, 1985), whereas the skeletons of monotremes retain many reptilian features (Mckay, 1894; Howell, 1937). The relation between the features of the brachial plexus and any other features of monotremes such as locomotor pattern requires further study.

ACKNOWLEDGEMENTS

This study was supported by a grant from the Japan Society for the Promotion of Science and the Australian Academy of Science, which we acknowledge gratefully. We thank Professor Gordon Grigg in the Department of Zoology, University at Queensland, Australia, for permitting and arranging the study of monotremes in that department, and Dr Frank Carrick and Dr Lyn Beard for providing the valuable platypus and echidna specimens used in this study. Emeritus Professor Jiro Kikkawa in the Department of Zoology, University of Queensland, kindly afforded Dr Koizumi an opportunity to study in that department. We also wish to thank the many colleagues who have provided kind assistance.

REFERENCES

Ballard WW (1964) *Comparative Anatomy and Embryology*, pp. 432–437. New York: Ronald Press.

Bolk L (1902) Beiträge zur Affenanatomie. III. Plexus cervico-brachialis der Primaten. *Petrus Campter* **1**, 371–566.

Brodal A (1969) *Neurological Anatomy in Relation to Clinical Medicine*, 2nd edn, pp. 145–150. New York: Oxford University Press.

Chiba S (1984) Morphological studies of the so-called Adachi's C-type brachial plexus. 2. Fasciculation of the plexus and segmental constitution of the nerve (in Japanese with English summary). *Acta Anatomica Nipponica* **59**, 707–722.

Dyck PJ, Low PA, Stevens JC (1988) Diseases of peripheral nerves. In *Clinical Neurology*, vol. 4 (ed. Joynt RJ), pp. 1–126. Philadelphia: J. B. Lippincott.

Gaupp E (1899) *A. Ecker's und R. Wiedersheim's Anatomie des Frosches*, Abt. 2, pp. 167–187. Braunschweig: Friedrich Vieweg und Sohn.

Haines RW (1939) A revision of the extensor muscles of the forearm in tetrapods. *Journal of Anatomy* **73**, 211–233.

Harris W (1939) *The Morphology of the Brachial Plexus with a Note on the Pectoral Muscle and its Tendon Twist*. London: Oxford University Press.

Homma T, Sakai T (1991) Ramification pattern of intermetacarpal branches of the deep branch (Ramus profundus) of the ulnar nerve in the human hand. *Acta Anatomica* **141**, 139–144.

Howell AB (1937) Morphologenesis of the shoulder architecture. Part V. Monotremata. *Quarterly Review of Biology* **12**, 191–205.

Jenkins FA Jr (1970) Limb movement in a monotreme (*Trachyglossus aculeatus*): a cineradiographic analysis. *Science* **168**, 1473–1475.

Kato K, Sato T (1984) Innervation of the levator scapulae, the serratus anterior, and the rhomboideus in crab-eating macaques and its morphological significance. *Anatomischer Anzeiger* **157**, 43–55.

Kerr AT (1918) The brachial plexus of nerves in man, the variations in its formation and branches. *American Journal of Anatomy* **23**, 285–395.

Kodama K, Kawai K, Okamoto K, Yamada M (1987) On the cutaneous branch of N. suprascapularis in lemur (in Japanese). *Medicine and Biology* **114**, 131–135.

Koizumi M (1989) A morphological study on the coracobrachialis muscle (in Japanese with English summary). *Acta Anatomica Nipponica* **64**, 18–35.

Koizumi M, Sakai T (1995) The nerve supply to coracobrachialis in apes. *Journal of Anatomy* **186**, 395–403.

Manners-Smith BA (1894) On some points in the anatomy of *Ornithorhynchus paradoxus*. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London* **1894**, 694–715.

Mckay WJS (1894). The morphology of the muscles of the shoulder-girdle in monotremes. *Proceedings of the Linnean Society of New South Wales*, 2nd Series **9**, 263–360.

Miller RA (1934) Comparative studies upon the morphology and distribution of the brachial plexus. *American Journal of Anatomy* **54**, 143–175.

Paterson AM (1887) The limb plexuses of mammals. *Journal of Anatomy and Physiology* **21**, 611–634.

Pridmore PA (1985) Terrestrial locomotion in monotremes (Mammalia: Monotremata) *Journal of Zoology* (*London*) **205**, 53–73.

Schaeffer JP (1953) *Morris' Human Anatomy*, 11th edn, pp. 1118–1150. New York: Blakiston.

Schumacher, S von (1908) Zur Kenntnis der segmentalen (insbesondere motorischen) Innervation der oberen Extremität des Menschen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien*, Teil 3, **117**, 131–209.

Starck D (1982) *Vergleichende Anatomie der Wirbeltiere*, Bd. 3, pp. 498–505. Berlin: Springer.

Straus WL Jr (1941) The phylogeny of the human forearm extensors. *Human Biology* **13**, 203–238.

Westling C (1889) Anatomische Untersuchungen über Echidna. *Bihang till K. Svenska Vetenskapsakademiens Handlingar*, Bd. 15, Afd. 4, No. 3, 44–51.

Williams PL, Bannister LH, Berry MM, Collins P, Dyson M, Dussek JE, Ferguson MWJ (1995) *Gray's Anatomy*, 38th edn, pp. 1266–1274. London: Churchill Livingstone.

Woodburne RT, Burkel WE (1988) *Essentials of Human Anatomy*, 8th edn, pp. 112–116. New York: Oxford University Press.

Yamada TK (1986) Re-evaluation of the flexor digitorum superficialis (in Japanese with English summary). *Acta Anatomica Nipponica* **61**, 283–298.