Unpublished drawings of marsupial embryos from the Hill Collection and some problems of marsupial ontogeny

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Abstract

Some 80 year-old original drawings of intrauterine embryos, neonates and pouch young of marsupials by A. Cronin are presented which belong to the Hill Collection, Utrecht, but were never published. They comprise 11 drawings of the brush-tailed phalanger *Trichosurus vulpecula,* eight drawings of the koala *Phascolarctos cinereus,* two drawings of the common vombat *Vombatus ursinus* and one drawing of the red-necked pademelon *Thylogale thetis.* The external morphology of the early developmental stages of these specimens is compared with the inner morphogenesis of some organs, particularly of the fore-limb, shoulder girdle and sternal apparatus. Functional and evolutionary correlations are discussed.

Past and present of the Hill Collection

James Peter Hill was born on the 21st of February 1873 at Kennoway in Scotland. In 1889 Hill entered the University of Edinburgh to study Science. In 1892, although he had not yet graduated, he was appointed Demonstrator of Zoology and Botany at the Biology Department of Sydney University, Australia. Once there, he started to collect all kinds of animals for his courses and his own research; this marks the beginning of his collection. After his graduation to B. Sc. in 1898 Hill stayed in Australia until 1906, when he returned to England to become Professor of Zoology at the University College of London. In 1921 he was appointed Professor of Embryology and Histology at the same College. He retired in 1938 but continued his scientific work until his death on the 24th of May, 1954.

Hill's bibliography comprises 58 papers, the greater part of which particularly deals with the early development of marsupials and monotremes, in which he took a special interest. His research had one central theme, which he expressed as follows: "the data of embryology, properly interpreted, can and do furnish striking and demonstrative evidence of genetic relationships" (Hill 1932). An important part of his collection was assembled during his Australian period. In later years it was extended with species from Africa and South America, particularly by means of purchases, the bills of which are still to be found among the original Hill documents. Hill also personally collected material during expeditions, e.g. in Brasil in 1913. Although all classes of vertebrates are represented in his collection, the great majority of species belongs to the mammalian orders of the monotremes, marsupials and primates.

At the time of his death Hill's collection was partly in his own residence and partly at the London University. The fear that careless use and neglect would sooner or later entail the loss of the collection prompted Dr. Catherine J. Hill, Hill's daughter and herself an embryologist, to find ways to prevent this. Dr. P. D. Nieuwkoop, who was at that time Director of the Hubrecht Laboratory, agreed to house the collection in the Hubrecht Laboratory on the condition that it would be completely catalogued. The Hubrecht

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Laboratory already possessed another large embryological collection, assembled by Professor A. A. W. Hubrecht (1853–1915) mainly in the Indonesian Archipelago. It took Dr. Hill ten years to catalogue her father's collection. After she had completed this work, the collection was transferred to the Hubrecht Laboratory in 1967.

The Central Embryological Collection is still subdivided into two separate entities, the Hill Collection and the Hubrecht Collection. It consists of material stored in alcohol and in paraffin (ca. 2000 flasks), of microscopical slides (ca. 80 000), and of original catalogues, note-books, drawings, photographs and other documents. The material pertains to the normal development of more than 600 vertebrates species. In addition some special collections related to experimental-morphological investigations have been incorporated, e.g. the collections of Spemann, Mangold, Rotman, Raven and Grüneberg (collection of mouse mutants). All this material is expressly available for morphological, descriptive and comparative embryological investigations. A concise catalogue of the Central Embryological Collection has been edited by Dr. E. C. Boterenbrood (1977). A copy of this catalogue is available from Dr. G. C. Bangma, Curator of the collection.

Currently an increasing number of scientists use the collection for such studies. In this respect it is noteworthy that in 1911 both Hubrecht and Hill stood at the birth of the Institut International d'Embryologie, now called the International Society of Developmental Biologists (ISDB). It is satisfactory to see that after so many years the collections of these noted embryologists still serve the original aims of this Society and even provide new inspiration to present-day embryologists.

Drawings of marsupial embryos by A. Cronin

Apart from the written entries, the notebooks of J. P. Hill contain some photographs and many simple drawings of marsupial embryos, neonates and pouch young. However, only a few of these have actually been used in J. P. Hill's publications, for example simple outline drawings of *Perameles nasuta* (Hill 1898) and *Thylacis obesolus* (Hill 1901). A simple outline drawing of *Dasyurus quoll* was published, simultanously showing the

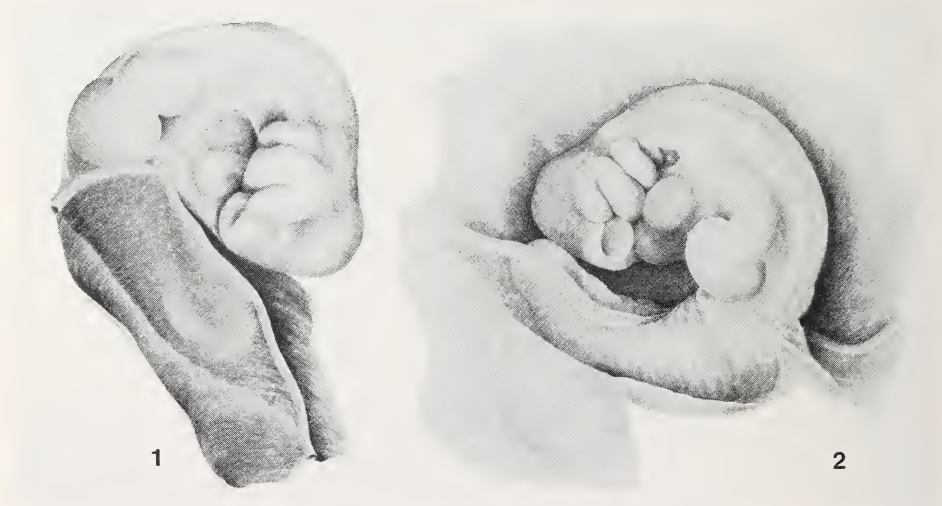

Fig. 1. Brush-tailed phalanger *Trichosurus vulpecula*, intrauterine embryos. 1: MS 253, 5 mm ?, 2: MS 250, 5.0 mm

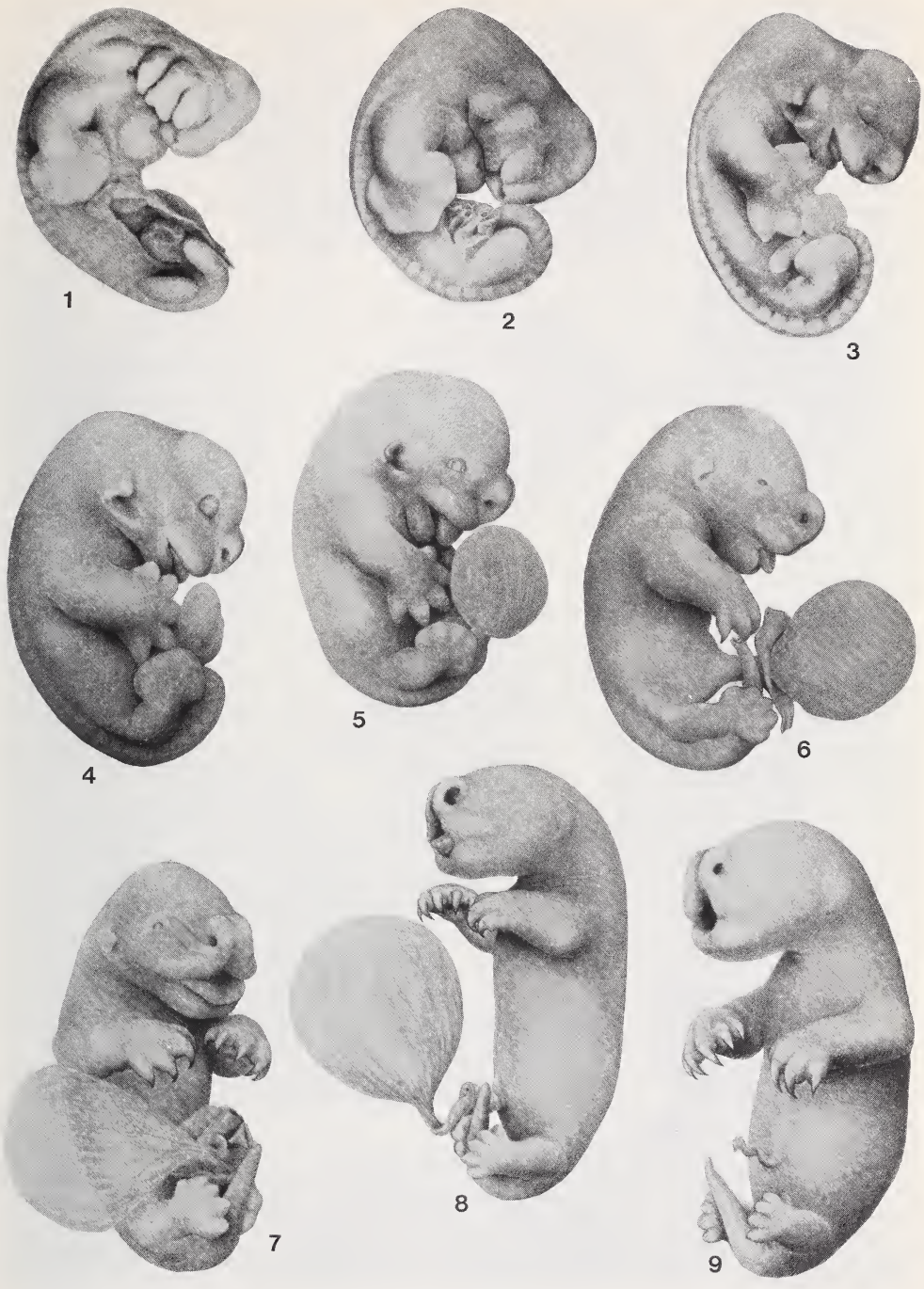

Fig. 2. Brush-tailed phalanger *Trichosurus vulpecula,* intrauterine embryos. 1: MS 257, 7.5 mm, 2: MS 259, 6.0 mm, 3: MS 257 ?, 7.5 mm, 4: MS 265, 8.5 mm, 5: MS 269, 10.25 mm, 6: MS 273, 11.5 mm, 7: MS 283, 14.0 mm, 8: neonate MS 286, 15.0 mm, 9: neonate MS 289, 15.0 mm

arrangement of the foetal membranes (Hill 1900). A number of very simplified drawings of intrauterine embryos, neonates and pouch young of *Trichosurus vulpecula* are contained in the work of Fraser and Hill (1915).

The only publication containing complete and detailed illustrations of the external shape of neonates and pouch young is the publication of Hill and Osman Hill (1955) on *Dasyurus quoll*. Obviously the authors were aware of the unusually good quality of these illustrations, because they wrote: "The beautifully executed pencil drawings of the pouch young . . . were made by Mr. A. Cronin of Sydney." However, it must be said that the reproductions in the quoted paper are not satisfactory, and that many delicacies were lost due to high-contrast printing. This is shown by comparison with the original drawings, 17 altogether, which are in the Hill Collection.

There are also other pencil drawings by A. Cronin in the Hill Collection, which to our knowledge have never been published. In reference to the Marsupialia there are some drawings of the ovary, the uterus, the foetal membranes and the placental structures and some additional drawings of complete intrauterine embryos, neonates and pouch young. Besides the 17 original drawings of the eastern dasyure *Dasyurus quoll,* mentioned above, there are 11 drawings of the brush-tailed phalanger *Trichosurus vulpecula,* two drawings of the koala *Phascolarctos cinereus,* eight drawings of the common vombat *Vombatus ursinus* and one drawing of the red-necked pademelon *Thylogale thetis*. Only a few drawings bear a signature. Nevertheless, their distinctiveness leaves no doubt that all of them were drawn by A. Cronin. The years of their production are uncertain, because they bear no date. However, we may assume that it must have been around the turn of the century, when J. P. Hill was in Australia collecting the embryological material. This assumption is also supported by the following note, taken from the publication of Hill and Osman Hill (1955): ". . . The material at our disposal was collected by one of us (J. P. H.) . . . during the years 1895–1905, when he was Demonstrator of Biology in the University of Sydney." Additionally, some of the drawings bear handwritten notes by J. P. Hill with annual dates between 1897 till 1902. Also going by the condition of the drawing paper one would judge their age to be between 80 and 90 years. The pencil drawings, measuring only 5–15 cm in length, have been carried out in a minute pencil-technique which reveals many details. The

Fig. 3. Koala *Phascolarctos cinereus,* intrauterine embryos. 1: MS 346, 7.5 mm, 2: MS 347, 9.0 mm

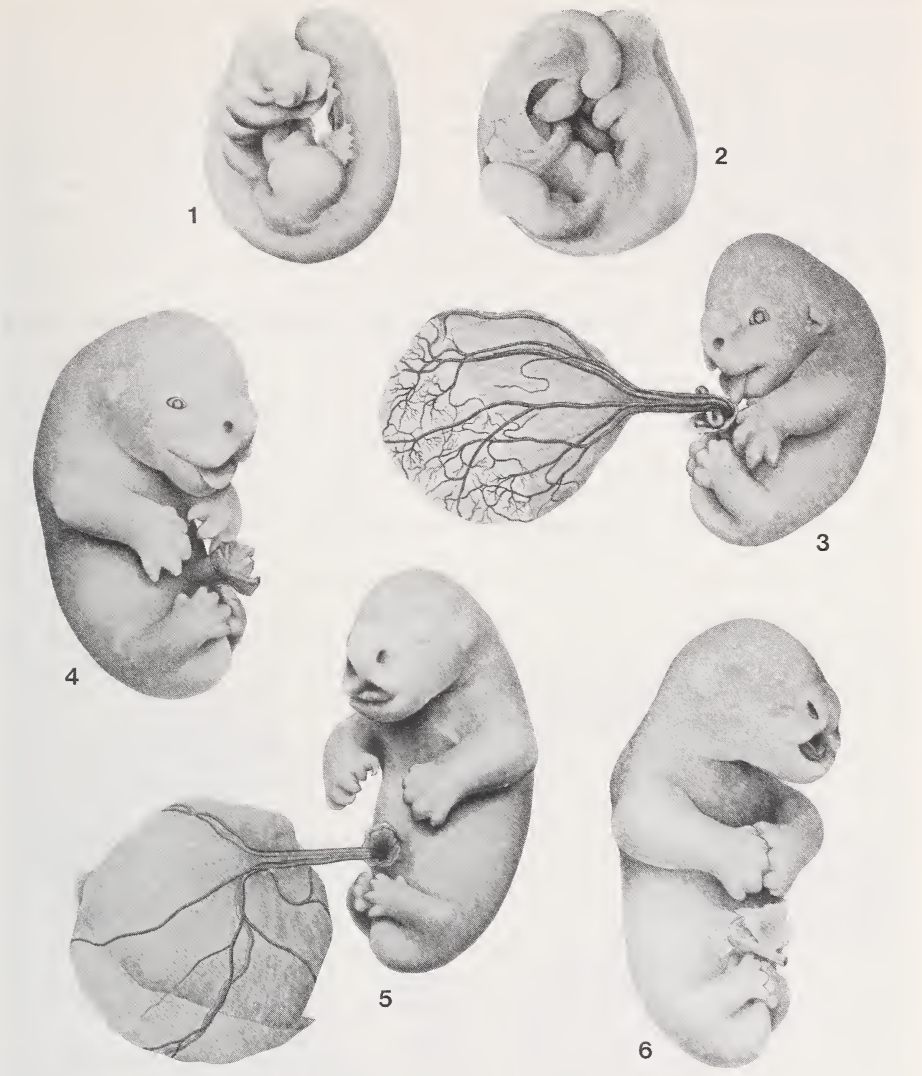

Fig. 4. Koala *Phascolarctos cinereus,* intrauterine embryos. 1: MS 345, 4.5 mm, right lateral, 2: left lateral view, 3: MS 348, 11.0 mm, 4: MS 350, 13.5 mm, 5: MS 351, 17.0 mm, 6: MS 352, 18.0 mm

appearance of the objects indicates that the drawings were made from fresh material or immediately after fixation. As most objects are very tiny i.e. about 5–15 mm long, there is no doubt that they had to be drawn with the aid of a magnifying glass or a microscope.

The drawings of marsupial embryos, neonates and pouch young by A. Cronin show a high degree of technical perfection and at the same time attest to the high artistic level of the artist. It is regrettable that they have not been published after their completion and therefore have remained without significance for science. Not only would they have enriched the store of knowledge at that time, they would also have been superior to the then technically imperfect photography. If we publish the drawings today, about 80 to 90

years after they were made, it is not for historical reasons only. They are in their way still much more instructive than some of the recent, technically sophisticated photographs. Additionally, there are not many published usefull depictions of marsupial embryonic stages and therefore we consider it appropriate to present the drawings to a larger public.

The most important reason for the publication of the drawings however, is that they depict individuals of which we have extensive series of microscopical slides. The drawings allow a comparison between the histological results and the exact rendering of the external morphology of the individuals examined. In this paper we attempt such a comparison with regard to the morphogenesis of the sternal-shoulder apparatus. This topic is treated in more detail in another contribution as well (Klima, submitted).

External morphology of the intrauterine embryos, neonates and pouch young of marsupials

Compared with the placentals, marsupials are born in a quite unusual condition. On the one hand they may be characterized as immature embryos, while on the other hand they are endowed with some highly specialized features. This led some authors to the conviction that they reflect genuine larval stages (Leche 1890). However, this opinion gained little approval. In any case "marsupials at the time of birth are true embryos, anatomically and physiologically. All species of marsupials give birth of tiny young, ranging in weight from 10 mg to about 750 mg. An individual neonate always has less then 0.2 % of the mother's body weight (1 % for the litter as a whole). Placentals in contrast are relatively much larger at brith, with individual neonates in small species comprising 2–3 % of the mother's body weight (20 % or more for the litter)." (Quoted from Lillegraven 1984, slightly changed with statements from Block 1964; Tyndale-Biscoe 1973; Eisenberg 1981; Millar 1981; Russel 1982.)

The most important features of marsupial neonates were summarized by Hill and Osman Hill (1955) in their investigation on *Dasyurus* as follows: "Notable at birth are 1. the relatively advanced state of the fore-limbs, 2. the presence of deciduous claws upon the manual digits and their later replacement by definitive claws, 3. the presence of the oral shield as a specialisation upon the muzzle, 4. the unique cervical swelling, 5. special features of the tongue and larynx, with the intranarial epiglottis, 6. the reptilian state of the lungs, 7. the advanced condition of the stomach and duodenum compared with the gut, 8. the state of development of brain and sense organs, the olfactory parts being especially forward in development, together with those parts of the nervous system necessary for controlling the movements of the fore-limb, sucking and respiratory movements, 9. the indifferent state of the gonads."

Many of these characteristics must, with no doubt be regarded as special adaptations to the unusual process of parturition in marsupials. Thus, despite its small size and immature developmental state the neonate has to achieve a remarkable performance at birth. "The life of the pouch young is a hazardous one, beginning with the long journey into the pouch on day 1. This blind and naked creature must grasp and crawl its way from the vagina to the marsupium, an average distance of 5 cm (in *Didelphis*), with no help from the mother other than the prebirth preparation which consists of licking and cleaning the genital and pouch area and the removal of the amnionic membranes" (Hunsacker 1977). In this process the neonate's fore-limbs play a decisive role. Compared with the body and the hind-limbs they are overproportionately large (Figs. 1–5). They are provided with pointed claws. They move alternately and by doing so drag the body in a wriggling manner together with the passively hanging minute hind-limbs. The whole distance from the vulva to the teat in the mother's pouch is managed solely through the power of the fore-limbs. The body as well as the hind-limbs behave passive in the process.

A rapid development of the anterior body half and the fore-limbs, respectively, may be detected even in the earliest developmental stages (*Trichosurus* Fig. 1: 1, 2; *Phascolarctos* Figs. 3: 1, 2 and 4: 1, 2; *Vombatus* Fig. 5: 1). Basically it is possible to observe a certain developmental predominance of the fore-limbs over the hind-limbs in the developmental process of all mammals. However, this is nowhere as pronounced as in the marsupials.

At birth the fore-limbs perform some kind of crawling movement (Hartman 1920; McCrady 1938; Hill and Osman Hill 1955; and others). This requires a powerful musculature and a solid skeletal support. Both have been demonstrated by the histological investigations. Among the muscle-groups this holds mainly for the pectoral musculature (Cheng 1955). The skeleton of the shoulder girdle forms a broad breast-shoulder arch, which requires a large space between the fore-limbs. This indeed corresponds to the external shape of both the late intrauterine embryos and the neonates. Between the fore-limbs a broad chestwall extends, which is sometimes well padded with a distinct muscle bulge. The distance between the fore-limbs is significantly large as is easily observed from the front in both intrauterine embryos and neonates (*Trichosurus* Fig. 2: 7, 9; *Phascolarctos* Fig. 4: 5, 6; *Vombatus* Fig. 5: 2). The bases of the extremities are located in the lateral trunk area. This lateral trunk position is typical reptilian. Most certainly it is advantageous for the crawling movements. The extremities will shift their positions from lateral to medial only postnatally in the pouch young, after the breast-shoulder arch has been reduced. Gradually they come to show the characteristically narrow "mammalian position" under the trunk.

The fore-limb digits are provided with sharp, bent claws. There are not yet definitive

Fig. 5. Common vombat *Vombatus ursinus,* intrauterine embryos. 1: MS 360, 9.0 mm, 2: MS 361, 15.5 mm. 3: Red-necked pademelon *Thylogale thetis,* intrauterine embryo MS 408, 17.0 mm

organs, but only provisional, non-permanent structures, which are usually termed "larval claws" (Hill 1900) or "deciduous claws" (Hill and Osman Hill 1955). They develop in late stages of intrauterine embryos and reach their maximum development at the neonate state (*Trichosurus* Fig. 2: 7, 8, 9; *Phascolarctos* Fig. 4: 5, 6; *Vombatus* Fig. 5: 2; *Thylogale* Fig. 5: 3). In the pouch young they are initially reduced and later replaced by definitive claws. Their organic function is clear, namely to keep a firm hold in the mother's abdominal hair during the crawling movements at birth (Barton 1806; Owen 1841; Beard 1897; Hill 1898, 1900, 1910, 1918; Hartman 1920, 1923, 1928, 1952; Langworthy 1928; McCrady 1938; Hill and Osman Hill 1955; a. a.).

The transitional appearance of claws during the short time period around birth reveals obvious parallels with the temporary appearance of the breast-shoulder arch. This is also a provisional structure, which comes into being in the late stages of intrauterine development and reaches its maximum development in the neonate, to be reduced immediately after birth. Both structures belong to the same adaptive system which allows typical marsupial birth in all its special aspects.

Early development of the shoulder girdle and sternal apparatus in marsupials

During marsupial embryogenesis the following structures can be recognized in the shoulder girdle and sternal apparatus: the scapula, the metacoracoid, the procoracoid, the first rib, the paired sternal elements, the unpaired sternal element and the clavicle. All these elements together form a compact, uninterrupted arch in both, intrauterine embryos and neonates. Immediately after birth, this arch is reduced in the pouch young. Then the solid connection between the left and right body halves ceases to exist, leaving only a loose connection via the clavicle. The metacoracoid becomes the processus coracoideus scapulae. The procoracoid becomes the praeclavium. The unpaired sternal element fuses with the paired ones into the uniform sternal manubrium. The first rib takes its usual position in the thorax. Thus the shoulder girdle and sternal apparatus as a whole show all the typical features of the adult marsupials as early as in the pouch young.

The embryonic shoulder girdle and sternal apparatus of the marsupials show strong similarities with the conditions in primitive monotremes. However, in the pouch young and in adult marsupials they generally reflect the conditions in the phylogenetically progressive placentals (cf. Broom 1897, 1899, 1902, 1912; Watson 1917; Hanson 1920; Romer 1922; McCrady 1938; Cheng 1955; McKenna 1961; Klima 1968, 1973, 1975, 1985).

The phylogenetically determined condition of the shoulder girdle and sternal apparatus during embryogenesis as a relatively primitive structure consisting of many elements is used functionally. In nearly all of the investigated marsupials the reduction of existing elements is delayed until after birth *(Dasyurus, Trichosurus, Phascolarctos, Vombatus, Petrogale, Thylogale, Wallabia, Macropus)*. The only exceptions are the peramelids *Thylacis* and *Perameles* (Klima, submitted). Accordingly, the neonates posses a solid arch, running straight from one side of the body to the other. This breast-shoulder arch serves many tasks: 1. Some of its parts, particularly scapula and sternum, offer an attachment surface for the mighty musculature which moves the fore-limbs. 2. In its extensive glenoid cavity, which is formed by the scapula and the metacoracoid, the enormous humerus head is solidly anchored. 3. Its medial parts, the sternum, the first rib and the metacoracoid, form a pressure-resistant structure that prevents the humeri from shifting medially when the huge pectoralis musculature contracts.

The morphogenesis of the shoulder girdle and sternal apparatus in marsupials takes place in the following manner: the paired structures initially originate in the lateral body wall and later slowly shift medially towards each other. Shortly before they reach the

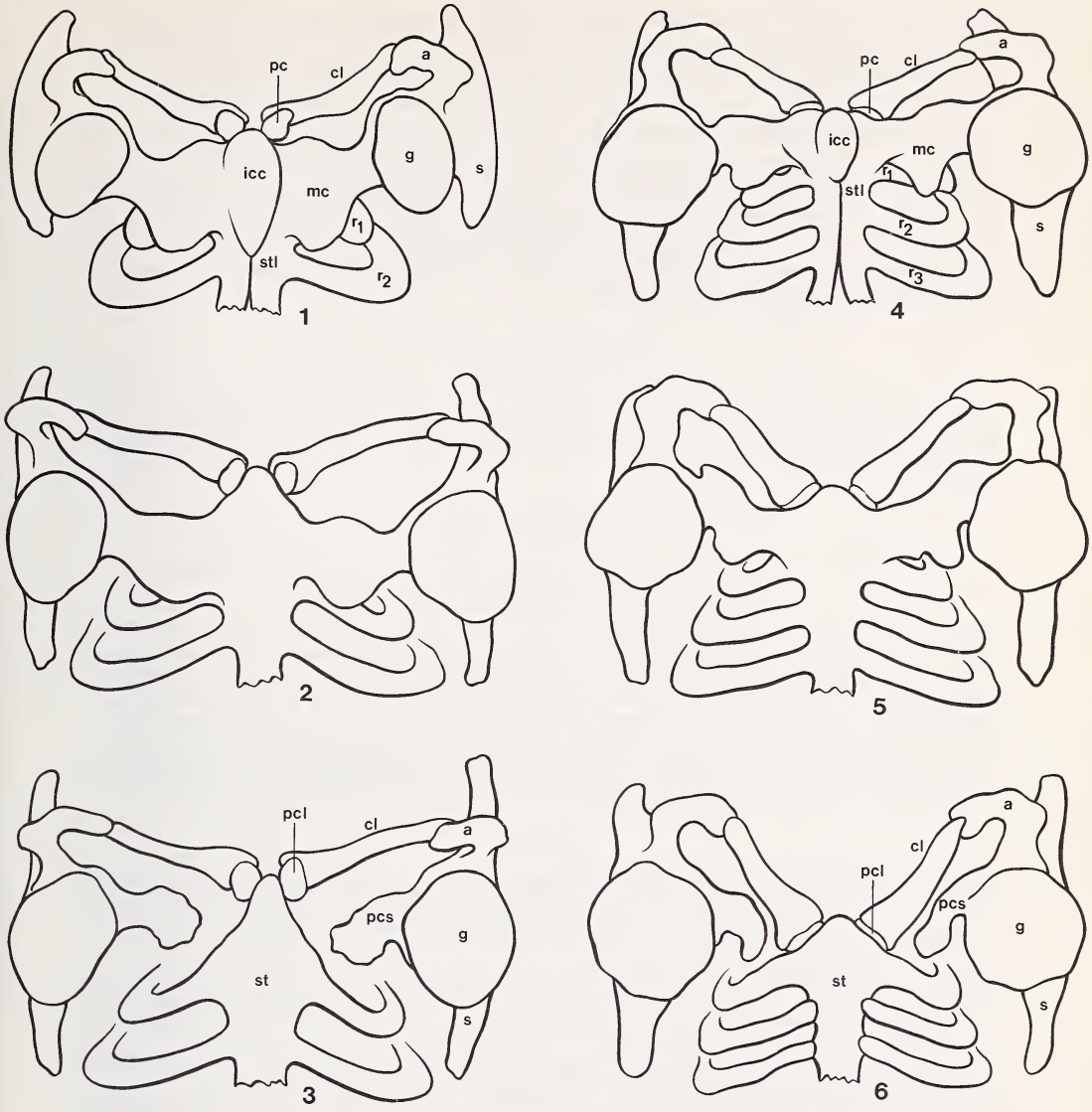

Fig. 6. Ventral view of the shoulder girdle and sternal apparatus. 1: Brush-tailed phalanger *Trichosurus vulpecula,* intrauterine embryo 12.0 mm, 2: intrauterine embryo shortly before birth 13.0 mm, 3: pouch young 17.5 mm. 4: Koala *Phascolarctos cinereus,* intrauterine embryo 12.25 mm, 5: neonate 16.5 mm, 6: pouch young 24.0 mm. Abbrev.: a = acromion; cl = clavicle; g = glenoid cavity; icc = unpaired sternal element; mc = metacoracoid; pc = procoracoid; pcl = praeclavium; pcs = coracoid processus; $r_{1,2,3}$ = ribs; s = scapula; st = sternum; stl = paired sternal element

medial plane, an unpaired structure is generated between them. It is indeed the initially unpaired chondral element of the interclavicle of ancestral forms which in the marsupials and placentals becomes the unpaired sternal element (Klima 1973, 1985). In the final stages of intrauterine development this process is readily visible insofar as the paired structures start to merge with the unpaired ones in the medial plane (*Trichosurus* Fig. 6: 1; *Phascolarctos* Fig. 6: 4). In due course the continually merging elements give rise to the

above mentioned continuous breast-shoulder arch. This reaches its maximum development in the intrauterine embryos and neonates immediately before and at birth (*Trichosurus* Fig. 6: 2; *Phascolarctos* Fig. 6: 5). Immediately after birth the metacoracoid begins to reduce, the sternum and first rib decrease in size, and the breast-shoulder arch is dissolved.

So even in the youngest pouch young there is no longer any solid connection of the body halves in the area of the shoulder girdle and sternal apparatus (*Trichosurus* Fig. 6: 3; *Phascolarctos* Fig. 6: 6). The fast reduction of the breast-shoulder arch is related to the further course of ontogenesis. While the pouch young develops further in the pouch its fore-limbs are barely used. Along with this decreasing functional significance, the initially overproportional size is reduced and the proportions will gradually change in favour of the hind-limbs (Sharman and Pilton 1964).

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Zusammenfassung

Unveröffentlichte Zeichnungen von Marsupialia-Embryonen aus der Hill-Sammlung und einige Probleme der Ontogenese von Marsupialia

Bisher unpublizierte Originalzeichnungen von intrauterinen Embryonen, Neugeborenen und Beutel-jungen von Marsupialia aus der Hill-Sammlung in Utrecht sind vorgestellt worden. Es handelt sich um etwa 80 bis 90 Jahre alte Bleistiftzeichnungen, Werke von A. Cronin aus Sydney. Es sind 11 Zeichnungen von Fuchskusu *(Trichosurus vulpecula)*, 8 Zeichnungen von Koala *(Phascolarctos cinereus)*, 2 Zeichnungen von Nacktnasenwombat *(Vombatus ursinus)* und 1 Zeichnung von Rothals-filander *(Thylogale thetis)*. Die externe Morphologie dieser frühen Entwicklungsstadien ist verglichen worden mit der inneren Morphogenese einiger Organe, insbesondere der vorderen Extremität, des Schultergürtels und des Brustbeins. Funktionelle und evolutive Zusammenhänge werden diskutiert.

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