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LACTATION IN MONOTREMATA AND SPECULATIONS
CONCERNING THE NATURE OF LACTATION IN CRETACEOUS
MULTITUBERCULATA

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The Monotremata are regarded as primitive mammals since they exhibit skeletal structures found in therapsid reptiles, and physiological processes and structures found in living Sauropsida. At the same time one finds in the monotremes characters as advanced as any in the Metatheria and Eutheria. Amongst these are parameters of lactation and structure of the mammary glands; those entities are discussed. Since researches of Kielan-Jaworowska (1971) have shown that Cretaceous multituberculates are more closely related to monotremes than to other Mesozoic mammals it is suggested that the parameters of lactation in multituberculates were similar to those of their living relatives—the monotremes. The notion is supported by the evidence (Kielan-Jaworowska 1979) that Cretaceous multituberculates had tiny altricial young as do the monotremes.

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LACTATION IN MONOTREMES

Monotremes are regarded as primitive mammals since they exhibit skeletal structures found in therapsid reptiles, and physiological processes and structures found in living Sauropsida. Examples of these are:

1. Ectopterygoids and post-temporal fossae in the skull.
2. Coracoids, precoracoids, and a median unpaired interclavicle in the pectoral girdle.
3. Epipubic bones in the pelvic girdle.
4. Cervical ribs.
5. Pylae antoticae and separate trabeculae in the chondrocranium.
6. Sclerotic cartilages around the eye cups.
7. Lagena macula in the cochlea which is uncoiled.

8. Oviparity; the yolk-laden eggs exhibiting a latebra, meroblastic cleavage, and a yolk navel at the bilaminar blastocyst stage.

9. An egg tooth on the premaxilla of the hatchling.

However, along with those conservative characters, some of which are known to occur in Mesozoic mammals one finds in the monotremes a host of mammalian characters as advanced as any of those found in metatherian and eutherian mammals (see Griffiths 1968, 1978). Among those advanced characters are the uptake of uterine secretions by the ovum, as in the marsupials, and the structure, physiology, and biochemistry of the mammary glands. In all three living genera of the Monotremata, *Ornithorhynchus*, *Tachyglossus*, and *Zaglossus*, each of the paired mammary glands consists of discrete club-shaped lobules bound together by connective tissue and arranged into the shape of a fan since the lobules are expanded distally but converge proximally, passing in the form of ducts through the abdominal wall (see Meckelio 1826, for *Ornithorhynchus*; Owen 1832, for *Tachyglossus*; Kolmer 1925, for *Zaglossus*). The ducts open to the exterior at two specialized patches of skin located on the ventral surface — the areolae. The areola is not just a patch of skin with holes through it, but it has a well-defined morphology: in the fully-lactating *Ornithorhynchus* the ducts below the skin are distended and resemble storage cisterns; peripheral to the ducts is a ring of convoluted glands resembling large sweat glands — the Knäueldrüsen of Gegenbaur. The whole areola is covered by a pélage of neighbouring and principal hairs (Nebenhaare, Haupthaare) the ducts opening to the exterior at the base of a principal hair the follicles of which are interspersed with sebaceous glands.

The two areolae in *Tachyglossus* are different from those of *Ornithorhynchus* in that they open dorso-laterally into a pouch which forms on the ventral surface during the breeding season and in that only a few hairs protrude from the surface of the areola; these are known as the mammary hairs (Bresslau 1920). The egg is incubated in the pouch for 10.5 days after which period the hatchling¹⁾ emerges and grows in the pouch by imbibition of milk for ca 50—60 days (Griffiths 1978). The areolae protrude above the surface of the skin of the pouch and internally they show the same structure as those in *Ornithorhynchus*: the ducts, expanded into sinuses, surrounded by a ring of Knäueldrüsen, open onto the flattened surface of the areola at the bases of the mammary hairs; the hair follicles are interspersed with sebaceous glands. The protrubent areolae in *Tachyglossus* resemble closely the nipples in woman; here the ducts also are expanded to form sinuses which open to the

¹⁾ The tiny hatchling structurally resembles very much the neonates of some marsupials: *Tachyglossus* females weigh 3—4 kg and their hatchlings ca 378 mg (Griffiths 1968) whereas a female *Macropus eugenii* (wallaby) weighs ca 4 kg and its neonatus 400 mg.

exterior on the flattened surface of the areola, Sebaceous glands are present along with a ring of convoluted glands surrounding the expanded ducts — the glands of Montgomery considered by Griffiths *et al.* (1973) to be homologues of the Knäueldrüsen. It is of interest to note here that just before eversion the marsupial teat anlage passes through a phase consisting of a plaque of epidermis and dermis exhibiting ducts, Knäueldrüsen (which persist in the adult), sebaceous glands and mammary hairs as is found in the areola of *Tachyglossus* (Bresslau 1920; Griffiths *et al.* 1972). The mammary glands in adult marsupials also exhibit discrete lobules bound together by connective tissue (Eggeling 1905; Griffiths *et al.* 1972).

Internally the lobules of the monotreme and marsupial mammary glands, and the mammary glands of the eutherians all consist of alveoli lined by a secretory epithelium.

Ultrastructurally the secretory cells are similar in all mammals prototherian, metatherian or eutherian (Griffiths *et al.* 1973). Each cell exhibits microvilli on the luminal surface of the alveolus, the base of the cell abuts onto a limiting membrane and myoepithelial cells. The nuclei of the secretory cells are large and rounded, the Golgi complexes and rough endoplasmic reticulum are very well developed. On the latter the characteristic protein of milk, casein, is first formed, is further elaborated in the Golgi complex, and is finally passed as the casein micelles into the lumen of the alveolus. Milk fat is secreted as a unit membrane-bounded droplet of triglyceride which balloons out into the alveolus and is finally nipped off and freed into the lumen of the alveolus. The secretory cells also synthesize a characteristic milk carbohydrate, lactose which occurs as the free disaccharide in the milks of many Eutheria (seal milks exhibit practically no carbohydrate). However the milks of Prototheria and of Metatheria contain little free lactose (Messer and Kerry 1973; Messer and Green 1979) but instead have oligosaccharides containing lactose and various monosaccharides.

From the above it is seen that the milks of all mammals contain the same proximate nutrients in the same forms—casein micelles, triglyceride droplets, and oligosaccharides. To those nutrients should be added minerals; one of special interest here is iron. All milks contain iron but from the data in Table 1 it can be seen that the amounts vary enormously from taxon to taxon. Thus the monotremes and the marsupials have far more iron in their milks than do those of eutherians. This is due to the fact that the hatchlings of the monotremes and the neonates of the marsupials are minute relative to those of Eutheria, consequently, in absolute terms the former have little iron in their bodies. Since they have to live for months on milk alone iron for haemoglobin, cytochromes, and myoglobin must be provided in the milk, hence the high concentrations.

The myoepithelial cells also are of especial interest; contraction of this

Table 1

Concentration of iron in the mature milks of various mammals

Species	Average Fe concentration mg/kg	Reference
Echidna (<i>Tachyglossus aculeatus</i>)	30.0 (range 12.6—47.8)	Griffiths (1978) and new data. Av. of 8 samples
Platypus (<i>Ornithorhynchus anatinus</i>)	19.0 (range 9.0—24.0)	New data av. of 6 samples
Quokka wallaby ¹⁾ (<i>Setonix brachyurus</i>)	23.8 (range 18.0—32.0)	Kaldor and Ezekiel (1962)
Tammar wallaby ²⁾ (<i>Macropus eugenii</i>)	14.9 (range 13.8—16.0)	Green and Newgrain (pers. comm.)
Marsupial cat ³⁾ (<i>Dasyurus viverrinus</i>)	16.6 (range 11.9—21.8)	Green and Newgrain (pers. comm.)
Woman	0.72 (pooled sample from 25 women)	Casey (1976)
Cow	0.33 ± 0.04	Casey (1976)
Goat	0.43 ± 0.12	Akinsoyinyu <i>et al.</i> (1979)
Mare	0.49 ± 0.06	Ullrey <i>et al.</i> (1974)
Ewe	0.92 ± 0.12	Ashton <i>et al.</i> (1977)
Rat ⁴⁾	4.50 (3.0—6.1)	Kaldor and Ezekiel (1962)

¹⁾ Young aged ca 70 days. ²⁾ Young aged ca 56–100 days. ³⁾ Young aged ca 47–187 days. ⁴⁾ Young aged ca 16 days.

tissue results in deformation of the alveolus which leads to a rise in intra-alveolar pressure thus squeezing the milk out into the ducts leading to the interior. This phenomenon is known as milk 'let-down' or ejection and the process is initiated in eutherians and metatherians (see Cross 1977; Lincoln and Renfree 1981) by the action of a nonapeptide, oxytocin, reflexly released from the posterior lobe of the pituitary gland by the sucking stimulus. Injection of oxytocin brings about milk ejection in Eutheria and Metatheria and also in the monotremes (Griffiths 1965, 1968; Griffiths *et al.* 1973). Furthermore it is known that the posterior lobe of the pituitary in *Tachyglossus* stores oxytocin (Acher *et al.* 1973) but as yet the identity of the nonapeptide in the posterior lobe of *Ornithorhynchus* has not been studied. Thus of one monotreme at least it can be said the mechanism of milk ejection is identical to that in Eutheria and in Metatheria. Furthermore the young of *Tachyglossus* suck in their milk so ejected just as any other mammal does (C.S.I.R.O. FILM 'COMPARATIVE BIOLOGY OF LACTATION, 1974); the flattened mouth opening on the ventral surface of the snout being admirably adapted to sucking from the flattened surface of the areola.

The mammary glands of the monotremes are not always full of actively secreting alveoli since both *Tachyglossus* and *Ornithorhynchus* are seasonal breeders. After weaning the glands decrease markedly in size and

regress to a solid, convoluted duct system. With the approach of the new breeding season the ducts grow and differentiate to a branched tubular grade of organization independently of pregnancy. If pregnancy supervenes and the glands are suckled the tubular system develops alveoli. Precisely the same series of events takes place in the mammary glands of a eutherian seasonal breeder introduced to Australia — the European Fox *Vulpes vulpes*.

SPECULATIONS CONCERNING LACTATION IN LATE CRETACEOUS MULTITUBERCULATA

It is appropriate to recall here some remarks made by Crompton and Jenkins (1979: 62) on the interpretation of the mammal fossil record for inference of behavioural, physiological and reproductive characters: "Some of these may be inferred by extrapolation from both paleontological and neontological studies although at present such conclusions are weighted with variable degrees of certainty".

From the facts outlined in the previous section it is apparent that the mammary glands and lactation of what may well be living representatives of Mesozoic mammals are as sophisticated as any in the Metatheria (with the exception of the Macropodidae who can make at the same time two kinds of milk for two young of different ages; see Griffiths *et al.* 1972) and in the Eutheria. One might surmise from this that Mesozoic mammals as highly evolved as the monotremes, as far as osteology is concerned, would have had equally sophisticated lactation. One group of extinct Mesozoic mammals, the taeniolabidoid multituberculates of the Upper Cretaceous of the Gobi Desert indeed approach to the Monotremata in some important aspects of their osteology. These mammals (*Kamptobaatar kuczynskii*, *Sloanbataar mirabilis*) as shown by the brilliant researches of Zofia Kielan-Jaworowska (1971) have more in common with the Monotremata than with any other Mesozoic mammals so far described. The principal criteria of similarity are the structures of the skulls in the two taxons:

In both groups the squamosals are narrow and do not contribute to filling in the side-wall of the brain case. The alisphenoids, ventrally located in both groups, are small in *Ornithorhynchus* but in *Tachyglossus* they do contribute significantly to filling in the side wall of the brain case as they do in *Kamptobaatar*. Most of the side wall however in *Tachyglossus* (Griffiths 1978) and in *Ornithorhynchus* (R. Presley pers. com.)²⁾ is filled in by ossifications formed within the membrana sphen-

²⁾ Griffiths (1978) from study of the skull of a fully-furred suckling platypus agreed with Watson (1916) and Vandebroek (1964) that the side wall of the brain case appeared to be filled-in by an anterior extension of the petiotic. However, Dr R. Presley of University College, Cardiff tells me that in earlier stages the side-

obturatoria and it would appear that this is so in the multituberculates (see footnote).

In both the monotremes and the multituberculates epipubic bones are present (Kielan-Jaworowska 1969), jugals are absent³⁾, cristae paroticae are present as are ectopterygoids and a post-temporal fossa (small in the tachyglossids) although in the monotremes there is no tabular. The tympanics are open and located ventrally; the cochleas are uncoiled and there is only one bone in the lower jaw — the dentary. Thus the suspension of the lower jaw is entirely mammalian exhibiting a dentary-squamosal articulation which in both groups, in ventral view, lies lateral to the ear region. In 1879 Doran wrote "I hardly need remind the anatomist that, as far as the ossicles are concerned the Monotremata wear a perfectly mammalian uniform, having malleus, incus, and stapes". The ear ossicles of multituberculates have not yet been found. However, it is very probable that their middle ears will prove to have malleus, incus, and stapes since there is no articular-quadrato suspension of the lower jaw and since even when this is present, along with a dentary squamosal articulation, in other Mesozoic mammals, there is reason to believe that the articular and the quadrato conducted sound waves to the cochlea (Crompton and Parker 1978; Kermack, Mussett and Rigney 1981).

Since the multituberculates and the monotremes have so much in common it is fair to surmise that the Mongolian multituberculates had mammary glands similar to, and as well-developed, as those of the monotremes. This notion is supported by the evidence (Kielan-Jaworowska 1979) that the late Cretaceous multituberculates had an extremely small neonate or hatchling. In the pelvis of *Kryptobataar dashzevegi* the left and right pubes and ischia form an acute angle so that the pelvis appears V-shaped when viewed from behind. The ventral edges of the opposite ischia and pubes are strongly fused together forming a ridge about 15 mm long indicating that probably the two sides of the pelvis could not be split apart under the influence of the hormone relaxin. The estimated greatest width of the ischial arc is about 4 mm so it is estimated that, if *Krypto-*

wall consists of a sheet of membrane bone in the spheno-obturator membrane not connected to the periotic at any point. In older specimens the periotic cartilage is invaded by ossification from the membrane bone giving the appearance of an anterior outgrowth from the periotic. It seems not unlikely that the bone filling-in the lateral wall in the Upper Cretaceous multituberculates is formed in the same way since Clemens and Kielan-Jaworowska (1979) point out that the bone consists of two parts arranged at right angles to one another.

³⁾ A knob of bone on the dorsal surface of the malar arch of a platypus was illustrated and labelled jugal by van Bemmelen (1901); Broom (1914) copied van Bemmelen's figure and both show a suture between the knob and the arch. I cannot detect such sutures in the malar arches of adult platypuses and furthermore there is no sign of a jugal at the clearly-visible suturing of maxilla and squamosal in a suckling platypus recently come to hand. I agree with Clemens and Kielan-Jaworowska (1979) that the monotremes lack jugals.

Table 2

Diameters of pelvic apertures in adult female platypuses

Body wt (kg)	Body length (cm)	Length of pelvis (ischio-pubic symphysis) (mm)	Diameter of pelvic aperture (mm)
—	46	11.0	16.0
—	45	10.5	14.0 ¹⁾
1.40	45	12.0	15.0
1.20	42	10.5	11.6
—	40	9.5	12.5
0.83	42	11.0	11.5 ²⁾
0.93	41	10.0	11.2 ³⁾

¹⁾ Soft parts present. ²⁾ Lactating, soft parts present. ³⁾ Lactating, soft parts present.

bataar was viviparous ⁴⁾ and allowing for the presence of soft parts, the maximum width of the head of a *Kryptobataar* neonate could be no more than 3.4 mm which is very small indeed compared with the head widths of the neonates of some marsupials. For example the average width of the head of new-born *Macropus eugenii* (weight of adult females ca 4 kg) is 4.6 mm (5 neonates) and average weight is 400 mg which is comparable to the weight of the echidna hatchling mentioned above. That the young of *Kryptobataar* were so small argues that they would have been suckled for a long time as are those of monotremes and of marsupials and that, therefore, *Kryptobataar* milk must have been rich in iron.

Concerning the structure of *Kryptobataar* mammary glands one might argue from the premise of the similarities of monotremes to multituberculates that it would seem not unlikely the milk formed in the alveoli of the *Kryptobataar* mammary gland was ejected by the action of the characteristically mammalian hormone, oxytocin, into expanded ducts or sinuses to open on a flattened areola rather than at a teat. However, Kielan-Jaworowska (1979) has advanced the notion that the long immobile symphysis and well-developed pelvic ridge may indicate that *Kryptobataar* was able to jump. If that were so it would be likely that the young were securely attached to teats as are those of very active and pouchless marsupials such as *Antechinus* species. However one can justifiably speculate that since all milks, prototherian, metatherian, and eutherian are basically alike, that *Kryptobataar* milk, whether imibed from teat or areola, contained casein micelles, fat globules, oligosaccharides and, since the neonate or hatchling was tiny, a high concentration of iron.

⁴⁾ See Addendum

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ADDENDUM

Kielan-Jaworowska (1979) showed it was unlikely that young with a head-width greater than 3.4 mm could pass through the narrow V-shaped pelvis of *Kryptobataar dashzevegi*. From this it was surmised that since the pelvis of the oviparous mammals are U-shaped and since cleidoic eggs as small as 3.4 mm in diameter are apparently unknown, that *Kryptobataar* probably was viviparous. However, this is arguable on a number of grounds:

(a) The pelvic aperture⁵⁾ including soft parts in adult platypuses can be as small as 11.2 mm (Table 2) whereas the diameters of laid eggs are 14×17 mm for single eggs and 13.8×17 mm for twin eggs (Burrell 1927). It is also apparent from the data in the Table that the smaller the platypus the smaller the pelvic aperture.

(b) The eggs of the living oviparous mammals have soft flexible shells allowing of distortion when passing through the small pelvic aperture. Distortion at this stage would not be deleterious to the embryo since it exhibits 19—20 pairs of somites only, and a head fold. The nutriment for further development during external incubation consists of, in the main, uterine secretions stored by the egg during a prolonged gestation period. Thus if an oviparous mammal exhibits long gestation and short incubation periods, quite small eggs could be laid.

(c) Cleidoic eggs of minimal diameter smaller than 3.4 mm are known: the oviparous scink lizard, *Menetia greyii* is on average only 33 mm long (snout-vent) and has a dorso-ventral thickness of 3.7 mm yet it lays soft distortable eggs of minimal diameter 3.0—3.3 mm and 4.4—7.3 mm long. At hatching tiny complete lizards emerge, capable of feeding themselves. The marsupial *Dasyurus viverrinus* gives birth to young weighing 12.5 mg and exhibiting a head-width of 1.75 mm, and the neonate of *Tarsipes spenserae* weighs only 2—3 mg⁶⁾, thus it is conceivable that *Kryptobataar* eggs of 3—4 mm minimal diameter could pass through the pelvis and produce a tiny hatchling like the neonate of *Dasyurus* or of *Tarsipes*.

(d) Finally it may be pointed out that marsupials such as *Phascogale tapoatafa* comparable in size to *Kryptobataar dashzevegi* (body weight 55 g estimated; Professor Zofia Kielan-Jaworowska pers. comm.) also have long V-shaped pelvises and that in the past these marsupials were probably oviparous since the embryos of *Trichosurus vulpecula* and *Phascolarctos cinereus* exhibit vestiges of an egg-tooth (Hill and De Beer 1949). Furthermore the blastocysts of all marsupials are encased in a keratinous egg shell for at least two thirds of their gestation periods.

In view of the above, oviparity in the multituberculates cannot be discounted.

⁵⁾ Determined by inserting wooden 'eggs' of various diameters into the aperture until one passed through.

⁶⁾ Personal communication Dr. C. H. Tyndale-Biscoe.

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