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Milk, Composition and Synthesis

GLOSSARY

casein micelle A white, colloidal aggregate that is found in milk and that is composed of several proteins together with calcium and phosphorus.

fat globule membrane The membrane that surrounds fat droplets of milk as they approach the apex of the plasma membrane of a milk-secreting cell.

Golgi apparatus A complex cytoplasmic organelle consisting of a series of layered fluid-containing sacs and associated small vesicles; involved in the delivery of cellular products to the cell surface or an intercellular destination.

secretory epithelial cell One of the system of mammary cells involved in the secretion of milk.

The common attribute that defines the vertebrate class mammalia is the production of milk, as the primary nutrient for the neonate, by mammary tissue. While the morphology and physiology of the mammary gland varies considerably from species to species, at the ultrastructural level the mammary epithelial cells have a common cellular motif. This cellular motif is quite adaptable, and by the regulation of its elements, each species can respond to a variety of nutritional circumstances and efficiently produce a milk with a composition suited to the requirements of its neonate.

I. INTRODUCTION

The virtual image of milk which would be constructed by most people is that of a creamy white

B. Other Reproductive Migrants

A few terrestrial reptiles are also known to make reproductive migrations. In each case it appears that the females are moving to an area which will improve developmental and hatching prospects for the offspring. In the Galapagos Islands, for example, some of the subspecies of the giant tortoise (*Geochelone nigra*) are known to migrate from foraging areas in the highlands down to the coastal lowlands to nest. The females travel well-worn tortoise trails to nest in sunny areas known as "campos" which have little vegetation and a silty soil. There are also two species of lizards which show short but interesting migrations. The young adults of the Australian ornate crevice dragon (*Ctenophorus ornatus*) migrate to larger granite outcrops for breeding purposes where they displace the young from the previous year in a repeating cycle of displacement and return migration. There is also a well-documented Panamanian population of *Iguana iguana* in which the adults undertake a short swim to a small island where a more protected breeding site can be found.

Among the Crocodilians the American alligator shows an interesting nesting behavior in which the female, after mating, often moves to a smaller pond away from the main population of adults. She builds a large nesting structure on land, deposits the eggs in the nest, and protects the area until the hatchlings emerge. It is thought that she does this to keep the hatchlings away from other adults (males?) that are known to eat the young alligators.

IV. PHYSIOLOGICAL CONTROL

Very little is known about the physiological control of migration in reptiles. We have hypothesized that testosterone in both the male and female may drive the initiation of the reproductive migration in sea turtles. Female loggerheads (*C. caretta*) monitored with radio tags and repeatedly recaptured over several months at Heron Island on the Great Barrier Reef of Australia showed a rise in testosterone as they left the foraging grounds for their nesting beaches. Olive ridleys, arriving from an open-ocean migration, similarly show elevated testosterone levels in the blood (Table 1) which drop to very low levels by the time of the final nesting for the season. In the several weeks prior to the migration, estrogen is elevated as the ovaries develop and testosterone is relatively low. Thus, the dramatic shift in these two steroids is most interesting and implicated in the behavioral changes required for migration. Males show an even earlier rise in testosterone and are well-known for departing to the mating areas prior to the females. In both sexes the testosterone levels in the blood drop gradually over the reproductive season until they are at much lower relative levels during the return migrations. Even though females often lay 2–10 clutches at about 2-week intervals, it appears that mating only occurs during a discrete receptive period prior to the onset of nesting. Once again, the males appear to begin the return trip first since males are rarely seen after the middle of the nesting season.

TABLE 1

Testosterone Levels in Sea Turtles in the Middle and at the End of Migration Season[a]

	Capture at First Nesting		Recapture at Last Nesting	
Turtle	*Date*	*Testosterone (pg/ml)*	*Date*	*Testosterone (pg/ml)*
1	Sept. 18/19	192.8	Nov. 24	16.7
2	Sept. 18/19	102.9	Not recaptured	
3	Sept. 18/19	187.6	Nov. 24	3.2
4	Sept. 18/19	205.8	Nov. 24	5.2
5	Sept. 18/19	224.3	Nov. 24	6.1
6	Sept. 18/19	299.6	Nov. 24	11.7

[a] Female olive ridley sea turtles from Costa Rica as shown in Fig. 3. A striking drop in testosterone levels is seen at the end of the nesting/migration season. Turtles returned to the deep ocean pelagic feeding grounds soon after the last nest (reproduced with permission from Plotkin *et al.* (1995) *Mar. Biol.* **122**, 137–143.

Acknowledgments

I thank Heather Kalb and Patricia Vargas for commenting on a draft of this article.

See Also the Following Articles

Migration, Amphibians; Migration, Fish; Reptilian Reproduction, Overview

fluid. The lubricity and taste of milk are related to this perception and are based on three unique biological structures: the colloidal calcium–protein complexes (the casein micelles), the milk fat globules with their limiting membrane, and the milk sugar, lactose. The complexity of these structures is necessitated by the fact that milk is in essence predominantly water. It is the accommodation of these ingredients to an aqueous environment that forms the basis for the structure of milk at the molecular level and calls for the unique secretory process of milk synthesis.

II. SYNTHESIS AND SECRETION OF MILK

A. Cell Physiology

The evolution of the mammary gland, presumably from external sweat glands, has yielded a great variety of exterior appearances in many species, but at the tissue level there is a common organizational theme as shown in Fig. 1a. Mammary secretory cells are epithelial in nature and are arranged in alveoli which are connected to ductal tissue. The secretory epithelial cells (SECs) are surrounded by a layer of myoepithelial cells, which are able to contract and expel milk into the ducts in response to the hormone oxytocin. The alveoli are highly vascularized to ensure a constant flow of the metabolic precursors needed for milk synthesis and secretion. Finally, the vascularized alveoli are embedded in an extracellular matrix. This matrix not only supports the cells but also through cell–cell interactions is responsible for the full expression of the genes that control milk synthesis.

B. Protein Synthesis and Secretion

Adaptation of milk components to their ultimate aqueous environment begins during secretion. Lipid and protein synthesis are partitioned from the start. Amino acids and their metabolic precursors are actively transported into the SECs and assembled into proteins on the ribosomes of the highly developed

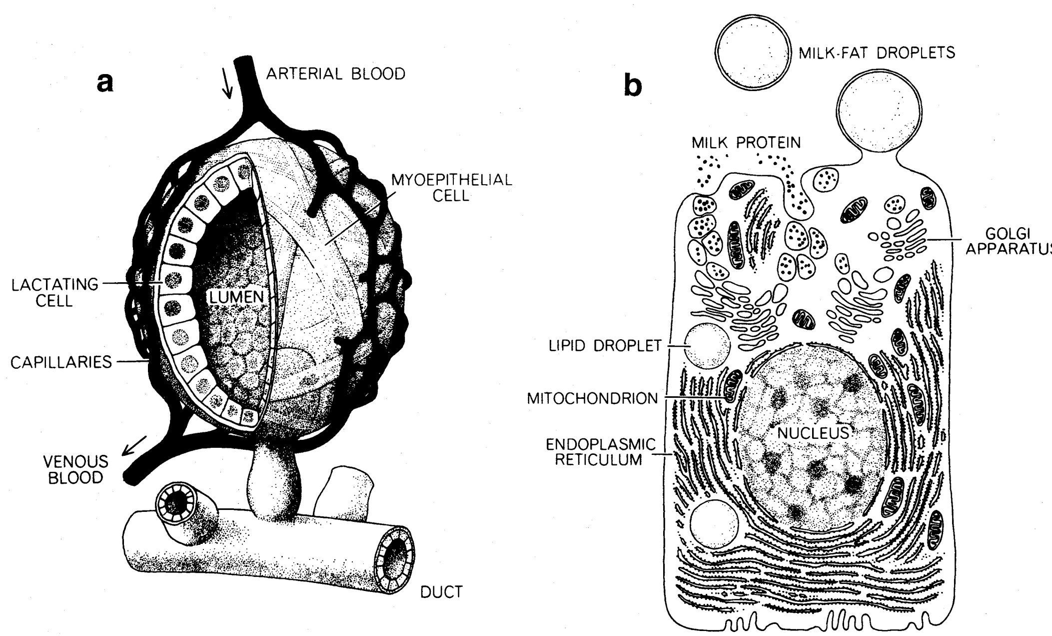

FIGURE 1 Cell physiology of lactating mammary gland. (a) A single alveolus consisting of lactating epithelial cells (SECs) surrounding the lumen. (b) A typical lactating cell indicating active secretion of protein and lipid by distinct mechanisms (reprinted with permission from S. Patton, *Sci. Am.*, July 1969).

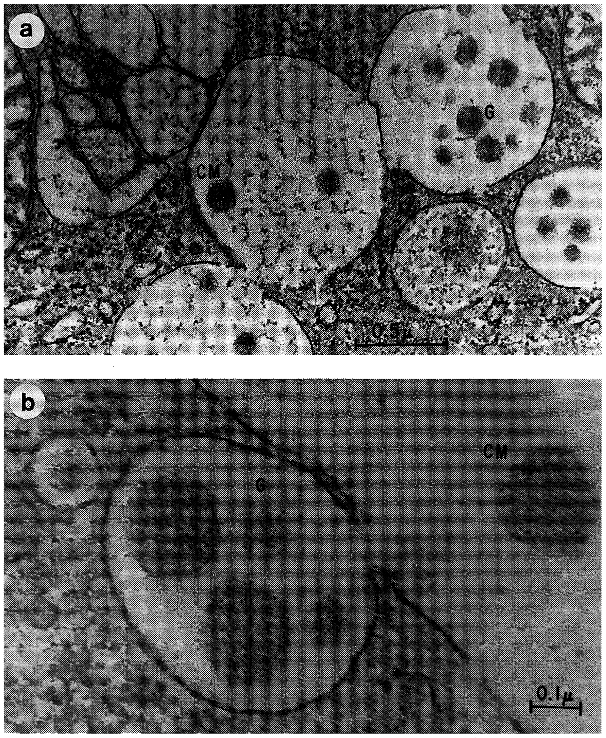

FIGURE 2 (a) Formation of casein micelles (CM) within Golgi vacuoles (G) and the aggregation of small submicellar particles into larger micelles. (b) A Golgi vacuole about to discharge its contents into the alveolar lumen; a CM is already present in the lumen (reproduced with permission from Farrell, 1988).

rough endoplasmic reticulum. All proteins of mammary origin have conserved leader sequences which cause insertion of the nascent proteins into the lumen of the endoplasmic reticulum (ER) shown in Fig. 1b. The proteins are then transported through the Golgi apparatus as shown in Fig. 1b; presumably the globular proteins of milk are folded during this period. In the Golgi apparatus, the caseins, which are the major milk proteins in most species, are phosphorylated to begin the process of calcium transport. In general, when milks that contain >2% protein are analyzed, the accompanying inorganic phosphate and calcium levels found yield insoluble precipitates (apatite or brushite). Conversely, in the absence of these salts, the casein components, as a result of their open structures, have a high viscosity. Thus, the gradual intercalation of calcium, casein, and phosphate into colloidal casein micelles ensures the effective transport of these vital minerals. This process can be visualized in Fig. 2a, in which small submicellar particles are seen in the secretory vacuoles nearest the *trans*-Golgi. Through the binding of calcium, which is actively transported by a Ca^{2+}-ATPase, and the accretion of phosphate, which is a hydrolysis product of nucleotide diphosphates, the colloidal casein micelles are formed and finally secreted by reverse pinocytosis (Fig. 2b).

C. Lactose Synthesis and Secretion

Another important biochemical event occurs in the Golgi apparatus: the synthesis of lactose from galactose and glucose. The Golgi membranes allow free transport of glucose but not disaccharides. The accumulation of lactose in the Golgi vesicles ensures the delivery of concentrated carbohydrate to the neonate. Interestingly, the water solubility of α-lactose at 30°C is 9.8%; primate milks at 7% lactose approach this limit. Lactose is found only in milks. This singularity is derived from the fact that the Golgi apparatus universally glycosylates proteins via the enzyme galactosyl transferase, but in the SEC the globular protein α-lactalbumin is inserted into the lumen of the ER and transported to the secretory vacuoles. In the secretory vesicles, the protein binds to galactosyltransferase and induces a modification of the active site to allow glucose to become the acceptor for galactose. Here a constitutive enzyme of the membranes has been subverted to carbohydrate synthesis. Lactose, α-lactalbumin, and the casein micelles are cosecreted in the Golgi vacuoles. It has been postulated that lactose acts as the primary osmoregulator in the secretion of the aqueous phase of milk (skim milk). Indeed, a "knockout" gene experiment on α-lactalbumin in mice virtually stopped milk synthesis. In marine mammals the lactose content is characteristically low, but the total protein contents are high, approaching 10% in some species. In many species (but not rodents and humans) β-lactoglobulin is the major globular protein cosecreted with lactose and casein. Currently, no incontrovertible evidence has been presented for a biological role for this globular protein; however, it has been postulated to be related to the calcium–phosphate balance necessary for casein micelle formation.

D. Lipid Synthesis and Secretion

At the onset of lactation there is an apparent increase in the lipoprotein lipase activity in the capillaries surrounding the SEC and a concomitant decrease of the enzyme in adipose tissue. The active lipoprotein lipase assures the SEC of a steady supply of dietary lipid for milk synthesis. Triacylglycerols constitute >98% of the milk fat of all species studied to date. Fatty acids with carbon numbers ≥16 are derived from the diet, whereas fatty acids with carbon numbers ≤16 are synthesized by the SEC. Dietary constraints and synthetic capability of the SEC determine the ratio of *de novo* synthesized to dietary fatty acid. Variations in the amounts and types of thioesterases present are responsible for the flavor notes created by the mixture of short-chain fatty acids common to some species. The hydrophobic lipid droplets form near the ER and are transported to the apical plasma membrane for secretion. As they traverse the cytosol, the growing lipid droplets, in accommodation to their aqueous environment, are encapsulated by a lipid monolayer that stains with osmium and contains enzymes and proteins that are cosecreted with milk lipids.

The secretion of protein, lactose, and salts in water (skim milk) appears to generate a surplus of apical plasma membrane. This surplus membrane either directly or indirectly gives rise to the milk fat globule membrane (FGM) that surrounds the fat droplets as they approach the apical plasma membrane as shown in Fig. 1b. Since the FGM is derived from SEC membrane, it shares many common properties with such membranes in that it contains phospholipids, cholesterol, and membrane-like proteins comprising a typical "unit membrane." However, the FGM has attached to it an inner coat that is thought to be proteinaceous and to bridge the gap between the inner phospholipids and the core triglycerides of the fat globules. The origin of this layer may be twofold: a portion arising from an inner coat of the plasma membrane and a portion arising from the interfacial layer that surrounds the nascent lipid globules. Since

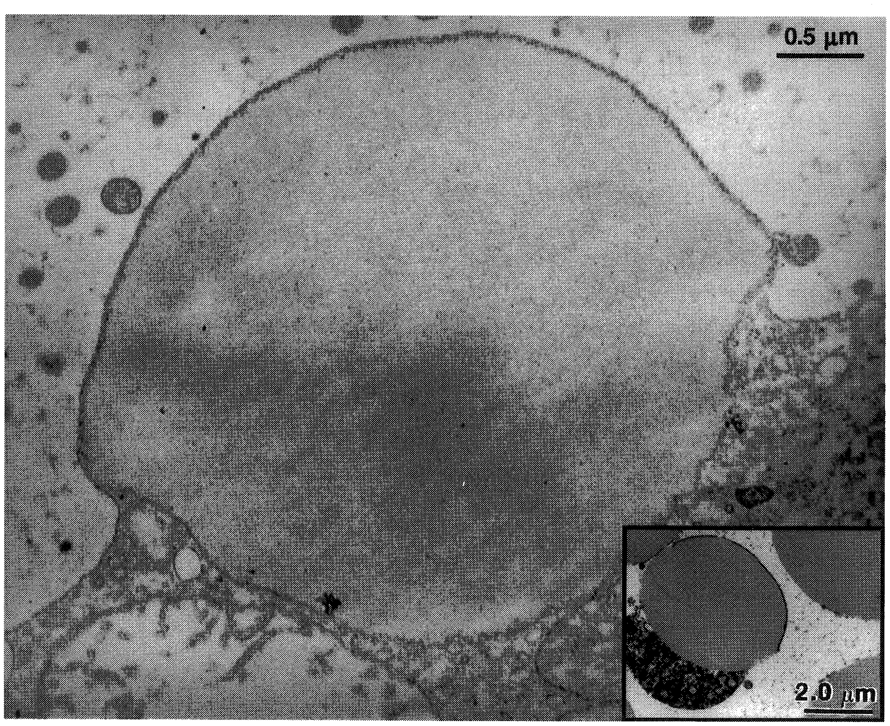

FIGURE 3 A fat globule passing through the plasma membrane of a secretory epithelial cell. The edge of the membrane shows the origin of the fat globule membrane (reprinted with permission from H. M. Farrell and M. P. Thompson, *J. Dairy Sci.* 54, 1219–1228, 1971). (Inset) Mature fat globule of human milk demonstrating the occurrence of "signets" of cytoplasm (reprinted with permission from R. J. Carroll *et al., Food Microstruct.* 4, 323–331, 1985).

the lactating mammary gland contains few active lysozomes, it has been theorized that there is little membrane recycling and that the surplus membrane generated by skim milk secretion is removed as FGM.

In the strictest sense, the secretion of milk can be defined as eccrine, in that after a cycle of protein and fat secretion the cells remain unchanged. In addition, well-developed tight junctions in the alveoli prevent direct leakage of serum components. A type of limited apocrine secretion occurs as well in that parts of mammary cells are often attached to the FGM. When fat globules are pinched off as shown in Fig. 3 where the plasma membrane clearly envelops the globule, pieces of cellular material can become entrapped with the globule. An example of such a cytoplasmic "signet" is shown for human milk in Fig. 3 (inset). The degree of signet formation varies considerably within and across species, with marsupial milks being highest.

III. COMPOSITION

A. Gross Composition

The composition of milk varies widely across species, with stage of lactation, and in response to diet. For the sake of comparison, the compositions of goat, cow, and human milk will be presented since they are well studied and of nutritional and commercial importance to most readers. The total solids contents of the three milks are approximately the same (Table 1). The major differences between the two ruminant milks and human milk arise from changes in the protein and lactose contents, which generally are negatively correlated. The major difference in protein content arises from the decidedly lower casein content of human milk. Indeed, the caseins are not the major proteins of human milk. The lower casein content is also reflected in the lower ash content because casein and calcium + phosphorus are positively correlated.

The total caloric values of the three are approximately equivalent (Table 2). Thus, for an adult, about 1 liter of unprocessed milk would supply much of a person's protein requirement and a sufficiency of calcium (depending on the excess chosen with respect to gender). Commercial milks are always fat adjusted to 3–3.5% fat depending on state requirements, and reduced fat products are also available. Thus, the caloric content of milk can be reduced while maintaining the calcium level; the majority of this mineral is associated with the caseins in the skim milk phase (Table 2). For an infant, about 1 liter of human milk (which is about the average daily yield of a nursing mother) supplies a good balance of protein, calcium, and calories. Both cow and goat milks are superabundant in nutritional content for infants and, accordingly, properly balanced infant formulas are constructed to take these concepts into account. It is important to note that the data given in Tables 1 and 2 are composite averages, and that individuals will differ from day to day.

B. Protein Composition

The dominant feature of skim milk is the casein micelle (Fig. 4a). This unique supramolecular aggregate imparts the opalescence characteristic of skim milk. As noted previously, the chief function of the

TABLE 1
Weight Percentage Composition of Goats, Cow, and Human Milk[a]

	Total solids	*Fat*	*Casein*	*Whey protein*	*Lactose*	*Ash*	*N*
Goat	13.2	4.5	2.5	0.4	4.1	0.8	2662
Cow	12.7	3.7	2.8	0.6	4.8	0.7	comp.
Human	12.4	3.8	0.4	0.6	7.0	0.2	comp.

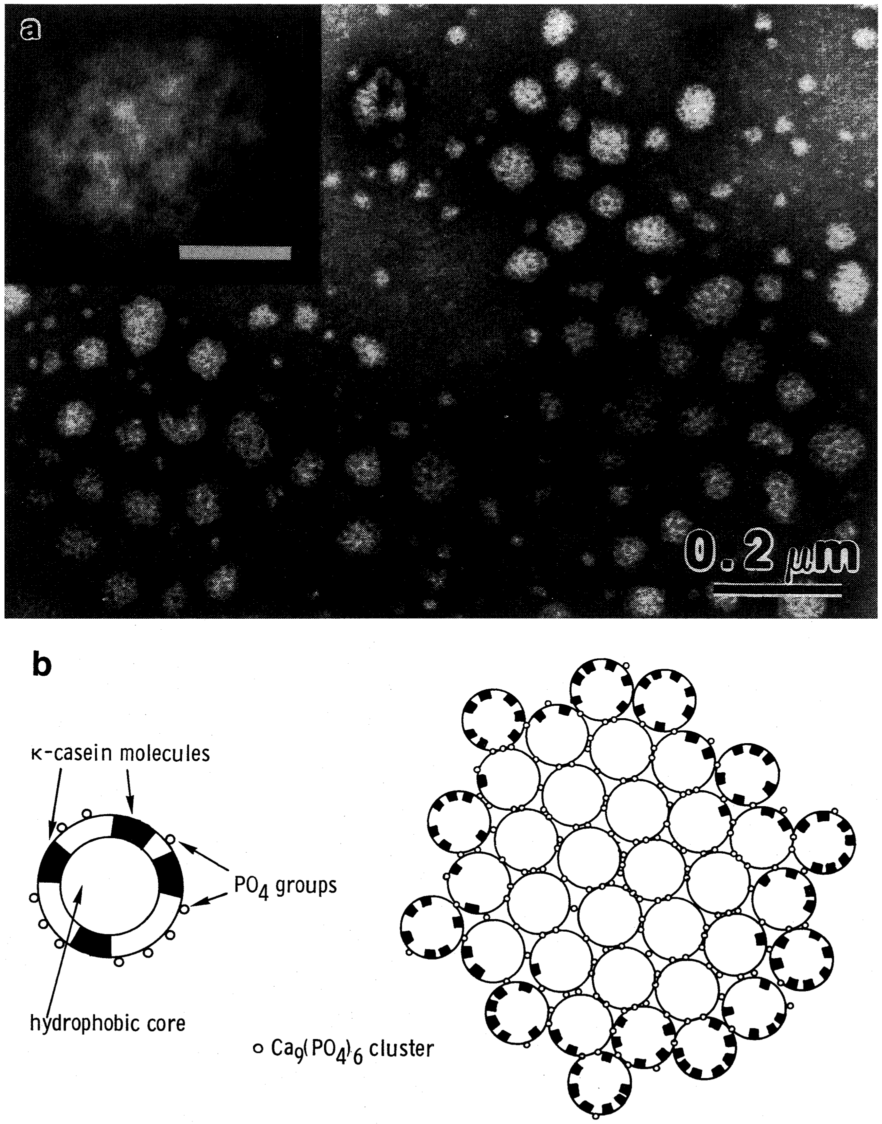

FIGURE 4 (a) Human casein micelles showing a wide range of sizes. (Inset) An enlarged micelle with well-defined submicellar structures (white particles). Scale bar = 30 nm (reprinted with permission from R. J. Carroll *et al.*, *Food Microstruct.* 4, 323–331, 1985). (b) Model for casein micelle structure (bovine) showing submicellar structure and surface arrangement of κ-casein [reprinted with permission from D. G. Schmidt, In *Developments in Dairy Chemistry-1*, *Proteins* (P. F. Fox, Ed.), Applied Science, London, 1982].

micelle is to fluidize the protein and solubilize the calcium and phosphate. From research on the characterization of the caseins of cows' milk, four major casein components are recognized: α_{s1}-, α_{s2}-, β-, and κ-casein. Caseins studied by protein or gene sequencing have been found to be homologous to these proteins in all species examined to date. The α_{s1}-, α_{s2}-, and β-casein are precipitated by calcium at the concentrations found in most milks. However, κ-casein is not only soluble in calcium but also interacts with and stabilizes the other calcium caseinates to initiate formation of the stable colloidal state. The casein micelle is thought to be composed of spherical aggregates of the individual caseins (submicelles) that are

TABLE 2
Nutritional Values of Milk Compared to Recommended Dietary Allowances

Dietary component	RDA		Supplied by 1 liter of milk		
	Adult[a]	*Infant*[b]	*Goat*	*Cow*	*Human*
Energy (calories)	2700 (M) 1925 (F)	650	678	650	648
Protein (g)	65 (M) 55 (F)	13	29	34	10
Calcium (g)	0.8	0.4	1.38	1.44	0.32
Phosphorus (g)	0.8	0.3	.72	.72	0.16

[a] 80-kg male >25 years; 60-kg female >25 years.
[b] 6-kg infant at 6 months.

held together by calcium–phosphate linkages. κ-Casein is thought to predominate on the micellar surface (Fig. 4b). In milk clotting in the stomach, the enzyme chymosin (rennin) specifically cleaves one bond in κ-casein to initiate aggregation of the micelles. At the ultrastructural level, the casein micelles of most species appear similar; however, the proportions of the various caseins vary widely. In goats, there is a high degree of variance in casein proportions among animals, which appears to be genetically controlled (Table 3).

In analogy with blood, the clotting of milk *in vitro* by chymosin leads to the generation of a milk serum. Milk serum can also be generated by ultracentrifugation or dialysis. All three methods yield similar products. Acid precipitation during cheese production yields a different product, richer in calcium, called whey. Milk serum contains some caseins and salts not associated with the micelles as well as lactose and the whey (globular) proteins of milk. The major whey proteins of mammary origin are α-lactalbumin, β-lactoglobulin, and lactoferrin; serum albumin and immunoglobulins are derived from blood by passive and active transport, respectively. In addition, there are a wide variety of milk components related to the biological origins of milk. These components arise from SECs, white blood cells (leukocytes) that move to the mammary gland during infection, and blood components that diffuse passively into milk through damaged tight junctions in the secretory alveoli.

TABLE 3
Percentage of Various Caseins in Milk

Milk	α_{s1}	α_{s2}	β	κ
Goat[a]	5–17	6–20	50	15
Cow[a]	38	10	40	12
Human[b]	Trace	*n*	70	27

C. Lipid Composition

When whole milk is either centrifuged or allowed to stand quiescently, a cream layer separates from the skim milk. The cream phase contains the fat globules, surrounded by FGM, and an aqueous phase similar to skim milk. The diameters of the fat globules range from 1 to 15 μm, but there is considerable variation across species. In freshly secreted milks, the FGM contains virtually all the polar lipids and cholesterol found in milk (~1% of total lipid) as well as true membrane-associated proteins. Pooling and processing of milk can lead to changes in lipid distributions. The major mammary-derived membrane protein has been called butryophilin; this protein may be a transmembrane protein and thus is

TABLE 4
Quantitative Analysis of Phospholipids of Goat, Cow, and Human Milk[a]

	% Phospholipid[a]		
Phospholipid	*Goat*	*Cow*	*Human*
Phosphatidyl ethanolamine	33.3	25.5	31.8
Phosphatidyl serine	6.9	5.8	3.1
Phosphatidyl inositol	5.6	4.4	4.7
Phosphatidyl choline	25.7	27.6	34.5
Sphingomyelin	27.9	31.9	25.2

[a] From W. W. Christie, *Developments in Dairy Chemistry—2 Lipids* (P. F. Fox, Ed.), Applied Science, London, 1983.

found on the luminal side of the FGM as well as in the inner coat. The relative compositions of polar lipids are given in Table 4.

The triacyl glycerides, at >98% of the total, dominate the lipid composition of all species. Differences arise in the individual fatty acids of the triglycerides. These differences are due to dietary, seasonal, and species influences. Typical distributions of the major fatty acids found in goat, cow, and human milk are given in Table 5. For the ruminants, the distribution of fatty acids is highly influenced by the biohydrogenation processes that occur in the rumen and lead to saturation of feed lipids. For monogastric animals such as humans, milk fatty acids are more directly influenced by changes in diet on a day to day basis. The appearance of $C_{18:1}$ in ruminant milk is due to the occurrence of an active Δ-9 desaturase in mammary tissues.

TABLE 5
Comparison of the Fatty Acid Distribution of Milk Trigylcerides[a]

	Weight (%)		
Me ester	*Goat*	*Cow*	*Human*
C_4	2.0	3.3	Trace
C_6	2.5	2.1	Trace
C_8	3.4	1.1	Trace
C_{10}	11.3	3.0	1.6
C_{12}	5.0	2.9	6.9
C_{14}	12.1	9.0	8.5
C_{16}	27.8	24.0	20.9
$C_{18:0}$	7.4	13.2	7.3
$C_{18:1}$	27.6	33.3	39.5
$C_{18:2}$	2.7	3.8	10.1
$C_{18:3}$	Trace	Trace	1.3

[a] From W. W. Christie, *Development in Dairy Chemistry—2 Lipids* (P. F. Fox, Ed.), Applied Science, London, 1983.

See Also the Following Articles

LACTATION, HUMAN; LACTATION, NONHUMAN; LACTOGENESIS; MAMMARY GLAND DEVELOPMENT; MAMMARY GLAND, OVERVIEW; MILK EJECTION

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Milk Ejection

Jonathan B. Wakerley

GLOSSARY

afferent pathway A neural pathway carrying impulses (usually derived from the nipples) toward the oxytocin-releasing cells of the hypothalamus.

bursting activity A brief episode of high-frequency firing characteristically displayed by oxytocin neurons prior to milk ejection.

hypothalamic oxytocin pulse generator The hypothalamic circuitry (including the oxytocin neurons themselves) responsible for the generation of oxytocin pulses during suckling.

milk transfer The process by which milk is moved from the mammary gland to the buccal cavity of the offspring.

neuromodulators Substances other than conventional fast-acting neurotransmitters that alter the electrical activity of neurons.

nursing The act of feeding the offspring by enabling them to suck the nipples.

sucking The action of holding the nipple in the mouth and applying rhythmical negative pressure.

suckling Strictly, a synonym for nursing. However, it is frequently used as an interchangeable term for sucking.

Milk ejection refers to the active process by which recently synthesized milk held within the mammary gland is actively ejected and thereby made available to the sucking young. This process is also referred to as "milk letdown" or "the draft." It is important to appreciate that milk secretion within the lactating mammary gland occurs as a continuous process, and the newly secreted milk is stored within the mammary alveoli or in specially modified parts of the duct system (Fig. 1). Because of the effects of surface tension, milk within the alveoli cannot be removed solely by sucking and has to be actively ejected by the action of special contractile cells called myoepithelial cells (Fig. 2). The process of milk ejection (galactokinesis) is therefore quite separate from milk secretion (galactopoiesis) and is under separate physiological regulation. Active milk ejection is needed for successful nursing in all mammalian groups, although in ruminants a portion of the milk is stored in a large cistern within the udder, from where it can be passively removed. Milk ejection is controlled by a neuroendocrine mechanism referred to as "the milk-ejection reflex," which is activated in response to suckling. When the offspring suck the nipples, the excitatory stimulus is transmitted to the hypothalamus to cause release of the hormone oxytocin from the posterior lobe of the pituitary. Oxytocin circulates to the mammary gland where it causes contraction of the myoepithelial cells and ejection of the milk. The milk-ejection reflex is often regarded as a "classical" example of a neuroendocrine reflex and continues to provide an invaluable model for understanding the organization of other less accessible neuroendocrine systems. This article covers all aspects of milk ejection but concentrates especially on the afferent control and organization of the hypothalamic oxytocin neurons. These are key areas in understanding operation of the milk-ejection reflex, and still are a focus of much research.