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MAMMARY GLAND ANATOMY NOTES

Mammary Gland Anatomy Notes: Cow to Cat (PDF)

A mammary gland is a greatly modified sweat gland, and where an animal carries hers was settled before she was born by a line of ectoderm running from the axilla to the groin. That one fact decides the whole comparative pattern: the cow, the ewe, the doe and the mare keep only the inguinal part of the line and consolidate their glands there into an udder, while the sow, the bitch and the queen keep the whole line and carry a chain from the chest to the groin. This guide takes the gland apart in that order — what kind of gland it is, the names of its parts, the path milk takes from a 200-alveolus lobule through the lactiferous ducts to a sinus divided by the annular fold, the two ways a lactocyte secretes, the teat and its three closing mechanisms, then the species pattern and the single developmental fact that decides how many holes a teat has. It finishes with what holds a full udder on, where the milk vein comes from, the lymph and the nerves, and the life cycle from ridge to involution. Inside: Fourteen labelled figures, ten reference tables and a 104-question self-test.

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IN SHORT

The cow has four mammary glands, the mare and the ewe two, the sow fourteen and the bitch ten — and the number, the position and even the count of holes in a teat were all settled before birth by a line of ectoderm called the mammary ridge. The gland itself is a greatly enlarged apocrine sweat gland: alveoli lined by lactocytes, wrapped in myoepithelial cells, draining through lactiferous ducts into a sinus that is divided by the annular fold into a gland part and a teat part. An udder is not an organ but a position — glands consolidated in the groin, held by elastic medial and fibrous lateral laminae, fed through the inguinal canal by an external pudendal artery that may exceed 15 mm, and drained by a milk vein that exists only because the valves of two separate veins failed during the first pregnancy.

KEY POINTS

1. **It is a sweat gland, and that is not a metaphor.** Dyce places the mammae in the chapter on the common integument and calls them greatly modified, much enlarged sweat glands; the histologists classify the gland specifically as a modified **apocrine** sweat gland. Everything else follows: it is ectodermal, its architecture is a skin gland's scaled up, and its position was decided by a line drawn on an embryo.
2. **The mammary ridge decides where, and how many.** A linear ectodermal thickening runs from the axilla to the groin in the embryo. How much of it persists decides the region — the whole line in carnivores and the pig, the **groin only in ruminants and horses**, the thorax in women. How many buds survive on it decides the gland count. Buds that should have regressed and did not are supernumerary teats.
3. **An udder is a position, not an organ.** It is what you call mammary glands that are consolidated in the groin into one mass. A cow's udder is **four glands**, each with its own duct system, its own sinus and its own teat. The word is also applied to the sow's much more separated glands, which is worth knowing so the term is not over-read.
4. **Alveolus, lobule, lobe, sinus — in that order.** About 200 alveoli make a lobule of roughly 1.5 × 1.0 × 0.5 mm; lobules make lobes; each lobe is drained by a collecting duct; and only **about ten or a dozen** wide lactiferous ducts finally enter the sinus. The ducts alternate wide and narrow, and the palpable dilations are called milk knots.
5. **The lactiferous sinus has two parts and a fold between them.** The gland sinus above and the teat sinus below, separated by the **annular fold**, which is built on a submucosal venous ring — the venous circle of Fürstenberg. Its prominence varies, and Dyce records that occasionally it is pronounced enough to impede milk flow. Together the two parts hold several hundred millilitres.
6. **One cell, two modes of secretion.** The lactocyte releases milk **fat** by the apocrine mode — the droplet leaves wrapped in a piece of the apical cell membrane — and milk **protein** by the merocrine mode, plain exocytosis, losing nothing of itself. Lactose goes with the protein; immunoglobulin A comes from plasma cells, not from the lactocyte at all.

7. **Nothing moves without the myoepithelial cell.** It lies between the alveolar cells and the basal lamina, carries contractile filaments and oxytocin receptors, and contracts to force milk into the ducts. The afferent limb of that reflex is the sensory nerve supply of the teat and udder skin; the efferent limb is oxytocin from the neurohypophysis. Adrenaline suppresses it, which is why a stressed animal holds her milk.
8. **Three things close a teat, not one.** A sphincter of smooth muscle reinforced by elastic tissue; a plug of fatty desquamated cells produced by the stratified squamous lining between milkings; and the longitudinal mucosal folds that let the canal close on itself. The rosette of Fürstenberg sits where the folds meet the teat sinus — and Dyce warns it is **rarely as distinct as traditionally described**.
9. **The orifice count is a developmental fact.** One epidermal sprout gives one duct system, one sinus, one papillary duct and **one orifice**. The cow, the ewe and the doe take that route; the mare and the sow have two sprouts and two openings per teat; the bitch has 10 or 12 and the cat 4 to 8. §7's table is not a list to memorise once §8's sentence is understood.
10. **Two laminae, two materials, one predictable failure.** The medial laminae are largely **elastic** and come from the tunica flava; the lateral laminae are **dense collagenous** tissue from the lateral crus of the inguinal ring. Because the elastic sheet stretches more, the medial part of a full udder sags and the teats point outwards and forwards. Dyce records that the apparatus occasionally ruptures.
11. **The milk vein is two veins whose valves failed.** In the heifer the cranial and caudal superficial epigastric veins drain separate territories in opposite directions. During the first pregnancy the increased flow distends them, the valves become incompetent, and the two unite into one channel that can carry blood either way — visible under the skin, entering the body wall at the palpable **milk well**.
12. **The genitofemoral nerve is the one to name.** Its cranial branch supplies the forequarters, its caudal branch the hindquarters, and it supplies the gland substance and the deep teat wall **alone**, reaching the udder through the inguinal canal. Lymph goes to one to three mammary (superficial inguinal) nodes — palpable between the thighs — and on to the deep inguinal node, which can be palpated per rectum.

> **About the images**
>
> Twelve figures are reproduced for educational reference: five from *Bovine Anatomy: An Illustrated Text*, 2nd extended ed. (the udder folios) and seven from *Dyce, Sack and Wensing's Textbook of Veterinary Anatomy*, 5th ed. (Figs. 10.33, 29.42, 10.32, 10.31, 29.40, 29.44 and 29.45). Each is credited beneath it and copyright remains with the original authors and publishers. The other two figures are diagrams of our own, drawn for this guide from the sources named under them.

01 What this page covers, and what it hands on

This is a comparative account of the normal mammary gland in the cow, the ewe and the doe, the mare, the sow, the bitch and the queen. It is written for a student who has to know how many glands a species has, how many holes are in a teat and why, what holds a full udder on, and which nerve carries the sensation that lets milk down — and who has to be able to say all of that for seven species rather than one.

The gland is worth this much attention because it is one of very few organs a veterinary student meets that is *built, used, taken apart and built again* on a schedule — the endometrium is the other — and because more of the working day of a farm-animal clinician is spent with a hand on one than on any other single structure. It is also, in the textbooks, oddly scattered: the comparative material sits in the chapter on the skin, the cow's udder sits four hundred pages later in the chapter on the bovine pelvis, and the mare's is in a third place again. This page puts them side by side.

What is here

Structure and comparison, in the order a reader can build on: what kind of gland it is, the names of its parts, the path milk takes from the alveolus to the outside, how the milk is actually made, the teat, then the species pattern — how many glands, where, and how many orifices per teat — and then support, blood, lymph, nerves, and the life cycle from the embryonic ridge to involution. Fourteen figures, ten tables and a self-test go with it, and the whole article is also a free PDF.

⛔ What is deliberately not here

Four things are left out, and each is left out for a reason:

- **Mastitis is left out as a clinical subject.** The anatomy that bears on it is here — that each quarter has its own duct system, that the teat canal holds a keratin plug between milkings, that quarters on the same side share tissue — and it is written as anatomy, with nothing about diagnosis, treatment or control attached to it.
- **Mammary tumours and their management are left to our page on cancer in animals.** The lymph drainage of the canine and feline mammary chain is here, because that is anatomy. Everything past it is not this page's subject.

- **Milking machinery and dairy production management are not this page's subject either.** Teat-end shape is described because it is anatomy that varies between normal animals; what a machine does to it is a different question and is not answered here.
- **Lactation endocrinology is not covered in its own right.** The hormones appear only where they explain a structural change — oestrogen before puberty, prolactin at lactogenesis, oxytocin at let-down — and no further.

Where the neighbouring pages are

If you want the udder inside the whole cow rather than on its own, our guide to bovine anatomy for veterinary students covers it in place, with the abdominal floor and the inguinal canal around it. If you want the comparative method applied across organs instead of within one, comparative veterinary anatomy, species compared does that. And the naming conventions this page leans on — why *papilla mammae* and "teat" are the same thing, and which of the two a written answer should use — are set out in our guide to veterinary anatomy terminology.

One note on sources, because it matters for how the numbers below should be read. Two books carry this article: *Dyce, Sack and Wensing's Textbook of Veterinary Anatomy*, 5th edition, and *Bovine Anatomy: An Illustrated Text*, 2nd extended edition. Where they disagree — and on one count they do — both are named and neither is quietly dropped.

02 It is a sweat gland: what that explains

Start with the classification, because almost everything else on this page follows from it. The mammary gland is not an organ in its own category. Dyce puts it in the chapter on the common integument, immediately after the sweat glands, and describes the mammae as *greatly modified, much enlarged sweat glands whose secretion nourishes the young*. The histologists are more specific still: it is a modified **apocrine** sweat gland with a specialised secretory function. Budras adds the qualifier that matters taxonomically — a modified skin gland that occurs in this form only in true mammals.

Three consequences follow immediately, and they are the reason to put this first.

- **It is ectodermal.** The gland, its ducts and the contractile cells that squeeze it are all derivatives of the epidermis, not of anything glandular that was there before — which is why this organ is filed under the integument rather than under the reproductive tract in the body systems of domestic animals.
- **Its architecture is a skin gland's architecture, scaled up.** Each gland is a compound tubuloalveolar gland: secretory end-pieces grouped into lobules, the lobules separated by connective-tissue septa that also carry the vessels and nerves in.
- **Its position was decided by a line drawn on an embryo**, not by the organ it feeds.

The mammary ridge, and why the udder is where it is

In the embryo, on each side of the ventral body wall, a linear thickening of the ectoderm appears between the primordia of the forelimb and the hindlimb. That is the **mammary ridge** — the "milk line". Budras notes that it is shifted ventrally as the dorsal part of the body wall grows faster than the ventral part, which is why the adult glands end up on the belly rather than on the flank.

Epithelial sprouts grow down from the ridge into the underlying mesenchyme, forming **mammary buds**, and each surviving bud becomes one gland. Two facts about the ridge then decide the whole comparative pattern:

- **How much of the ridge persists decides where the glands sit.** Dyce sets it out species by species: the ridge may run the whole way from the axilla to the groin, as it does in carnivores and the pig, or it may be of much more limited extent — restricted to the axilla in elephants, to the thorax in women, or to the **groin in ruminants and horses**.
- **How many buds survive decides how many glands there are.** More buds appear than survive. Most of the extra ones regress; some persist, and those are supernumerary teats.

That single sentence about ruminants and horses is the explanation of the udder. An udder is not a special organ: it is what a set of mammary glands looks like when the ridge that produced them was confined to the groin and the glands ended up consolidated there. §3 takes the word apart properly.

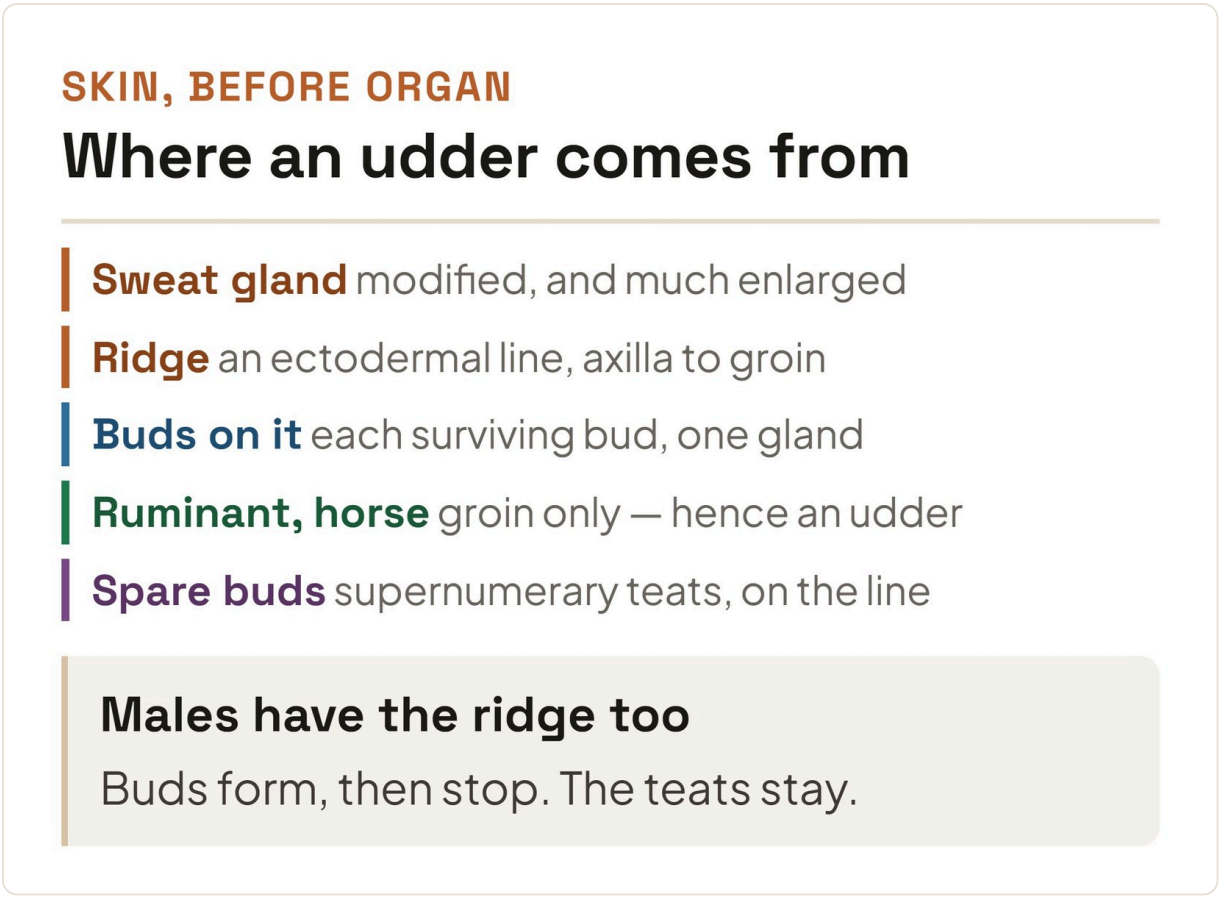

Fig 1 — What kind of gland it is, and what put it there The gland is a modified, much enlarged sweat gland; a line of ectoderm called the mammary ridge runs from axilla to groin in the embryo; each surviving bud on it becomes one gland; and the part of the ridge that persists decides where the glands end up. In ruminants and the horse only the groin part persists — which is what an udder is. Buds that survive where they were not wanted become supernumerary teats.

Diagram — Vet-eBooks.com, drawn for this guide. Data from Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed., ch. 10, and Budras K-D, Habel RE, Mülling CKW, Greenough PR. Bovine Anatomy, 2nd extended ed. Schlütersche, p. 88.

The teat is built two different ways

There is a developmental distinction here that is easy to miss and worth carrying. In ruminants and the horse the teat is a **proliferation teat**: Budras describes it as forming by the growth of the areolar tissue — the mesenchyme around the epithelial sprout — with the ring of skin around the bud completely taken up into the teat. The gland grows a teat outwards. That is a different process from the one that produces a nipple where the sprout's own opening is simply carried on the surface, and it is part of why a bovine teat is a long, thick-walled, cylindrical structure that a hand can work, rather than a papilla.

Colostrum, in one paragraph

The first secretion after parturition is not milk but **colostrum**, and its job is immunological rather than nutritional. It carries a high concentration of immunoglobulins, which give the newborn passive immunity; Budras adds that it is also laxative, and helps the newborn pass meconium. In the cow it is produced for about the first five days. This is the one piece of lactation physiology this page needs, and it is here because it explains why the gland exists in the form it does — and why the calf that does not get it is in trouble that no amount of later milk fixes.

03 The parts, named once: complex, gland, body, teat

Four words are used loosely in conversation and precisely in an examination — **complex**, **gland**, **quarter** and **udder** — and a reader who has not fixed them will lose marks that have nothing to do with anatomy. This section does nothing else.

One gland

A single mammary gland is a **body** plus a **teat**. Budras names them in Latin: the body is the *corpus mammae* and the teat is the *papilla mammae*. The body is the mass of glandular tissue with its duct system and its connective-tissue framework; the teat is the projecting part

that carries the milk to the outside. The relative size of the two varies with the individual, the species and the stage of lactation — a bovine teat, Budras says usefully, is about as thick as your thumb and about as long as your index finger.

Inside the body, the tissue is arranged in a strict hierarchy that is worth learning as a sequence rather than as a list, because the duct names follow it exactly:

TERM	WHAT IT IS	HOW MANY
Mammary complex	All the mammary glands of one animal, taken together The word says nothing about whether they are separated or consolidated	One per animal
Mammary gland *glandula mammaria*	One functional unit: a body of glandular tissue, its own duct system, and its own teat	Four in the cow, two in the mare, fourteen in the sow
Body *corpus mammae*	The glandular mass, with its ducts, sinus, framework, vessels and nerves	One per gland
Teat *papilla mammae*	The projection that carries the duct or ducts to the outside	One per gland in the cow; the mare has one teat per gland carrying two duct systems
Quarter	The bovine name for one gland, from the four-part appearance of the udder	Four — two fore, two hind
Lobe	A large division of the body of one gland, drained by one collecting duct	Numerous
Lobule	A bunch-of-grapes cluster of alveoli, about 1.5 × 1.0 × 0.5 mm, bounded by connective-tissue septa	About 200 alveoli in each
Alveolus	The secretory end-piece itself: a sac of lactocytes wrapped in myoepithelial cells	The unit that actually makes milk

The udder is a word for a position

This is the point at which most readers go wrong. An **udder** is not a type of organ and not a synonym for "mammary gland". It is what you call the glands of a species in which they are *consolidated in the groin into a single mass*. Dyce puts it exactly: the mammary glands in species such as ruminants and horses *may appear to merge in a single consolidated complex called the udder* — and then adds, honestly, that the term is also applied to the much more distinctly separated glands of the sow.

So the cow's udder is four glands, not one. The mare's is two. The ewe's and the doe's are two. Each keeps its own duct system, its own sinus and its own teat; what makes them an udder is that they are packed together in the inguinal region under a common skin.

Quarters, halves and the grooves between them

In the cow, the four glands are called **quarters**: two forequarters and two hindquarters. A median **intermammary groove** divides the udder into a right half and a left half, and that groove is real — it corresponds to the medial laminae of the suspensory apparatus, and §9 shows that the halves can be separated by blunt dissection along it. The boundary between a forequarter and a hindquarter on the same side is a different matter: Dyce says it is *rarely distinct*, and Budras notes there is no septum between them at all, even though their duct systems are entirely separate. Hold on to that asymmetry; §4 uses it.

The skin over the udder is thin, supple and easily slipped over the underlying tissue — except over the teats, where it is tightly bound down and naked. Budras adds that the udder skin is hairless and free of skin glands on the teat itself and sparsely haired elsewhere, and that the loss of that easy mobility is one of the things a clinician feels for.

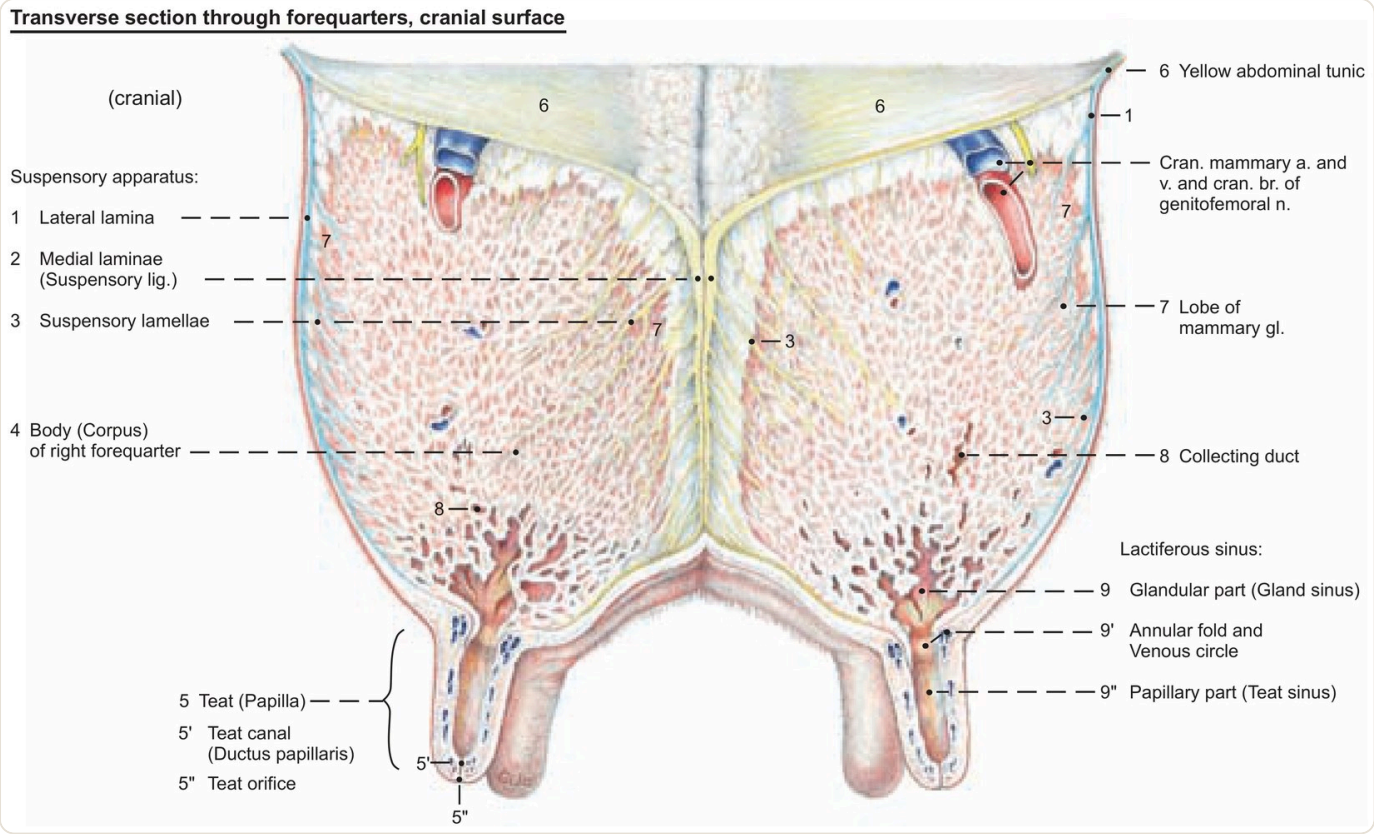

Fig 2 — The whole udder in one section, with the parts named A transverse section through the forequarters, cut so that both glands and both teats are in the plane. Working outward: 1 the lateral lamina and 2 the medial laminae of the suspensory apparatus, with 3 the lamellae running into the gland; 4 the body of the right forequarter; 5 the teat, 5' the teat canal and 5" the orifice; 6 the yellow abdominal tunic; 7 a lobe; 8 a collecting duct; and the lactiferous sinus in its two parts — 9 the gland sinus and 9" the teat sinus — separated by 9', the annular fold with its venous circle. Every one of those is a heading or a table row below.

Image — Budras K-D, Habel RE, Mülling CKW, Greenough PR. Bovine Anatomy, 2nd extended ed. Schlütersche — folio 89, upper plate: a transverse section through the forequarters of the udder. Reproduced for educational reference.

04 Inside: from the alveolus to the lactiferous sinus

Milk is made in one place and stored in another, and the route between them is the part of the gland a clinician reasons about most often. Follow it in one direction, from the smallest structure outwards, and the names look after themselves.

The alveolus and the lobule

The secretory unit is the **alveolus**: a sac lined by a single layer of secretory cells, the **lactocytes**, wrapped on the outside by contractile **myoepithelial cells** and set on a basement membrane. Alveoli are grouped into **lobules**, and the two books agree closely on the size of one: Budras gives about 1.5 × 1.0 × 0.5 mm and about 200 alveoli, and Dyce gives a lobule of 1 mm or a little more consisting of about 200 alveoli. Budras adds the comparison worth keeping: a lobule looks like a bunch of grapes.

One structural detail of the ruminant gland deserves its own sentence, because it is the reason a cow can be milked twice a day rather than continuously. Many alveoli open directly into one another, and the whole arrangement holds a large volume between milkings. Budras notes that this construction is what has led to the bovine gland being called a **storage gland**.

The duct orders

From the alveolus, the drainage runs through ducts of successively larger calibre and successively smaller number. Dyce sets out the bovine sequence: milk drains to an intralobular duct which joins others to form a larger interlobular duct; these lead into the system of **lactiferous** — milk-carrying — ducts, and the ducts of successive orders increase in diameter and diminish in number until **only about ten or so enter the sinus**. Elsewhere the same book puts the figure at *about a dozen* wide lactiferous ducts converging on the sinus; either way, the number a reader needs is that it is around ten, not hundreds.

SEGMENT	WHAT IT IS	WHAT IT DOES
Alveolus	A sac of lactocytes with myoepithelial cells outside them	Makes the milk and, when squeezed, empties into the next duct
Alveolar lactiferous duct	The first small excretory passage out of a group of alveoli	Collects from the alveoli of one lobule
Intralobular then **interlobular duct**	Successive unions inside and then between lobules	Gathers many lobules into one drainage line
Lactiferous duct	The wide milk-carrying ducts, with alternating dilated and narrow portions The dilations may exceed 3 cm and are the palpable milk knots	Carries and holds milk; the narrow portions' muscular walls keep it there until let-down
Collecting duct *ductus lactifer colligens*	One per lobe, opening into the gland sinus	Delivers a whole lobe's milk into the sinus
Gland sinus	The upper part of the lactiferous sinus, in the gland body	Stores milk between milkings; several hundred millilitres in total with the teat sinus
Annular fold	A mucosal fold on a submucosal venous ring, the venous circle of Fürstenberg	Marks the boundary; may be prominent enough to impede flow
Teat sinus	The lower part of the sinus, inside the teat	The reservoir the teat canal drains
Teat canal *ductus papillaris*	The last centimetre, through the teat wall to the orifice	Carries milk out, and is closed between milkings

The lactiferous ducts have a peculiarity that has a name in the parlour. They are, in Dyce's words, *unusual in demonstrating alternating wider and narrower sections*. The more superficial dilations may be 3 cm or more in calibre, can be felt through the skin when they are full, and are known as **milk knots**. The narrow portions have muscular walls, and their contraction holds milk in the expansions above until it is let down.

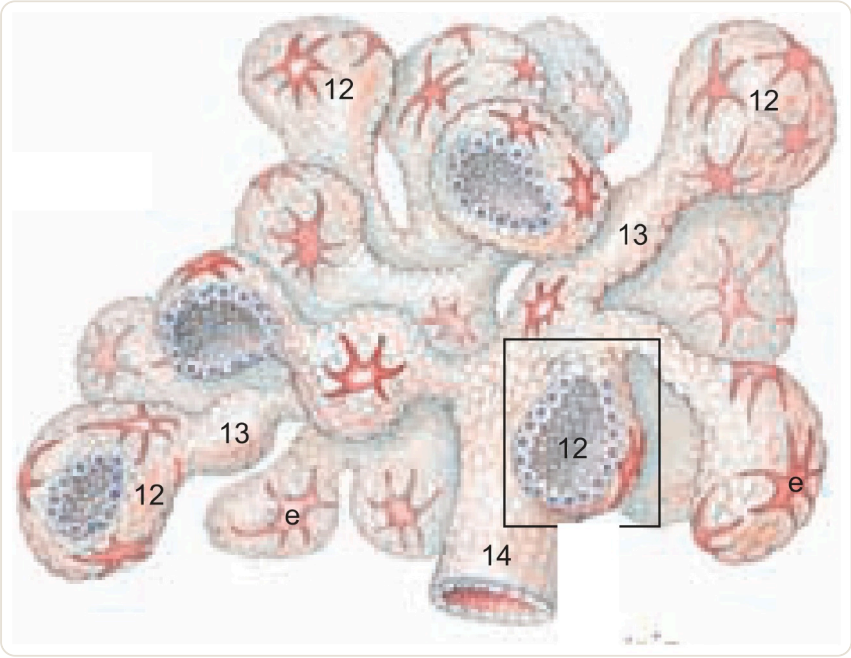

Fig 3 — One lobule, magnified The bunch of grapes: 12 marks the alveoli, 13 the alveolar lactiferous ducts that drain them, 14 the lactiferous duct they combine into, and *e* a myoepithelial cell lying on the outside of an alveolus. The boxed alveolus is the one magnified in the next figure but one. A lobule this size holds about 200 alveoli.

Image — Budras K-D, Habel RE, Mülling CKW, Greenough PR. Bovine Anatomy, 2nd extended ed. Schlütersche — folio 89, lower right plate: a lobule with its alveoli and alveolar lactiferous ducts. Reproduced for educational reference.

The lactiferous sinus, and the fold across it

All of that drains into one large cavity, the **lactiferous sinus** (*sinus lactifer*), which sits in the lower part of the quarter and continues down into the teat. In the cow its capacity is *several hundred millilitres*. It is not a single chamber: a mucosal fold runs across it and divides it into two

named parts.

The same cavity, under its other name

In a dairy context you will hear all three of these called **cisterns** rather than sinuses — Eurell glosses *sinus lactifer* as the **milk cistern**, the collection chamber. So the **gland cistern** is the gland sinus, the **teat cistern** is the teat sinus, and the **milk cistern** is the two of them together. Nothing anatomical changes with the word; the textbooks prefer *sinus* and the parlour prefers *cistern*, and you will be asked in both.

- The **gland sinus** (*pars glandularis*) is the upper part, inside the body of the gland. The collecting ducts open into it.
- The **teat sinus** (*pars papillaris*) is the lower part, inside the teat.
- Between them is the **annular fold**, and it is not just a fold of mucosa: it is built on a submucosal ring of veins, the venous circle of Fürstenberg. Dyce records that its prominence *varies*, and that *occasionally it may be sufficiently pronounced to impede milk flow*.

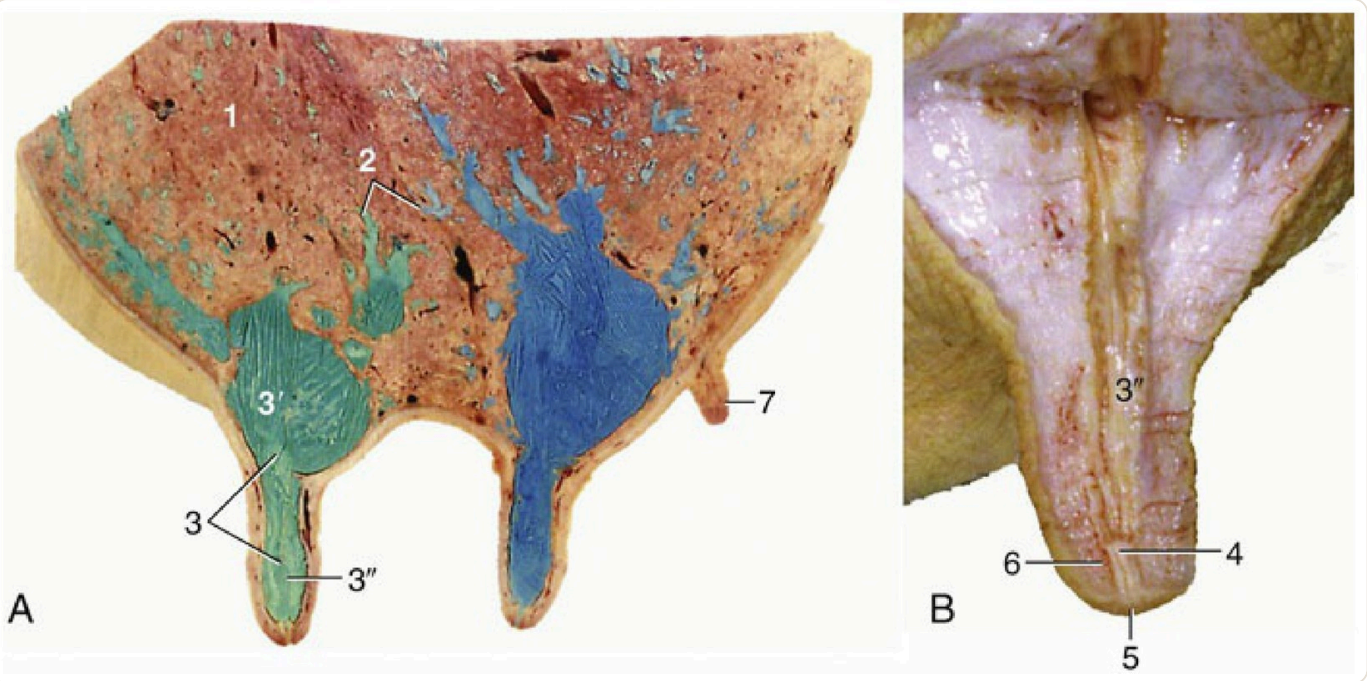

Fig 4 — The sinuses, filled with latex, and a teat opened (A) A sagittal section of an udder whose duct systems were injected with latex — green into the cranial quarter, blue into the caudal. The colours stop where the quarters stop, which is the demonstration that the duct systems do not communicate. 1 is the gland parenchyma, 2 the lactiferous ducts, 3 the lactiferous sinus with 3' the gland sinus and 3" the teat sinus, and 7 is a supernumerary teat. (B) An opened teat: 3" the teat sinus, 4 the papillary duct, 5 the orifice and 6 the sphincter.

Image — Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed. — Fig. 10.33, (A) a sagittal section of a latex-injected udder and (B) a section of the teat. Reproduced for educational reference.

How separate are the quarters, really?

This is the anatomical question underneath a great deal of clinical talk, and it has a precise two-part answer that is easy to state wrongly.

Two separate questions, two different answers

Are the duct systems separate? Yes, completely. Budras reports the demonstration: inject different coloured dyes into different quarters and each stays in its own quarter. Each bovine gland contains one duct system and its own glandular tissue — in contrast, Budras notes, to the bitch and the mare. Because of that, an infection ascending the teat canal is entering one quarter's plumbing, and Budras draws the anatomical conclusion carefully: it *may* therefore be limited to that quarter. **Is there a wall between neighbouring quarters?** On the same side, no. The two quarters of one side have no septum between them, and Dyce says the boundary between a forequarter and a hindquarter is rarely distinct. Between the right and left halves there is a real partition — the paired medial laminae — which is why one half of an udder can be removed surgically along that plane.

So the two statements sit at different levels. Down the *lumen*, a quarter is an island. Through the *tissue*, two quarters on the same side are continuous. That is the whole of what this page says about it; the clinical consequences are not this page's subject.

05 Two ways of secreting, and the cell that squeezes

The ducts are plumbing. This section is about what fills them, and it contains the one piece of terminology on this page that is genuinely a trap.

> **"Apocrine" means two things here, and both are true**
>
> The word is used twice on this page for two different ideas, and conflating them is the commonest confusion in this subject. **As a classification:** the mammary gland is a modified *apocrine sweat gland* — that is what kind of skin gland it is descended from. **As a mechanism:** the lactocyte releases milk *fat* by the *apocrine mode of secretion*, in which the droplet leaves wrapped in a piece of the apical cell membrane. The same cell releases milk *protein* by the **merocrine** mode — plain exocytosis, with nothing of the cell lost. So the gland is apocrine by ancestry and uses *both* mechanisms in service.

The lactocyte does two different jobs at once

The secretory cell of the alveolus is the **lactocyte**. It is not making one product by one mechanism; it is making several, and it releases the two biggest by two entirely different routes.

- **Milk fat leaves by the apocrine mode.** The lipids — predominantly triglycerides — arise inside the cell as small droplets that coalesce into larger ones. When a droplet is released it pushes out through the apical surface and takes a piece of the apical cell membrane with it, so the fat globule in milk is a droplet inside a membrane that used to be the cell's own. That is what apocrine release means.
- **Milk protein leaves by the merocrine mode.** The caseins and the whey proteins are made on the rough endoplasmic reticulum, processed through the Golgi apparatus, packaged into vesicles and released into the alveolar lumen by **exocytosis**. The cell loses nothing of itself.
- **Lactose** is a Golgi product too, and it has a distinction none of the others has: it is synthesised *exclusively in the mammary gland*. No other tissue in the body makes it.
- **Immunoglobulin A** is not made by the lactocyte at all. It is produced by plasma cells, either locally in the gland or arriving from the blood, and is transferred across the epithelium. It is abundant in colostrum.

COMPONENT	WHERE IT IS MADE	HOW IT LEAVES THE CELL
Milk fat Predominantly triglycerides	Arises as droplets in the cytoplasm, which coalesce into larger droplets	**Apocrine** — the droplet is released wrapped in a piece of the apical cell membrane
Milk protein Caseins and whey proteins	Rough endoplasmic reticulum, then processed by the Golgi apparatus	**Merocrine** — exocytosis of vesicles into the alveolar lumen
Lactose	A product of the Golgi apparatus, and synthesised **exclusively in the mammary gland**	Merocrine, with the protein fraction
Immunoglobulin A	Plasma cells — locally in the gland, or arriving from the blood	Transferred across the epithelium; abundant in colostrum

One caution about all of that: the height of the alveolar epithelium is not fixed. Dyce records that it *changes markedly during the cycle of activity*: the cells are tallest and most active in alveoli prepared to release milk, and after release the lumina are collapsed and irregular and the epithelium is much reduced in height. And the gland does not do this in unison — not all lobules within one gland are at the same stage, and active and inactive lobules can be found side by side in the same section.

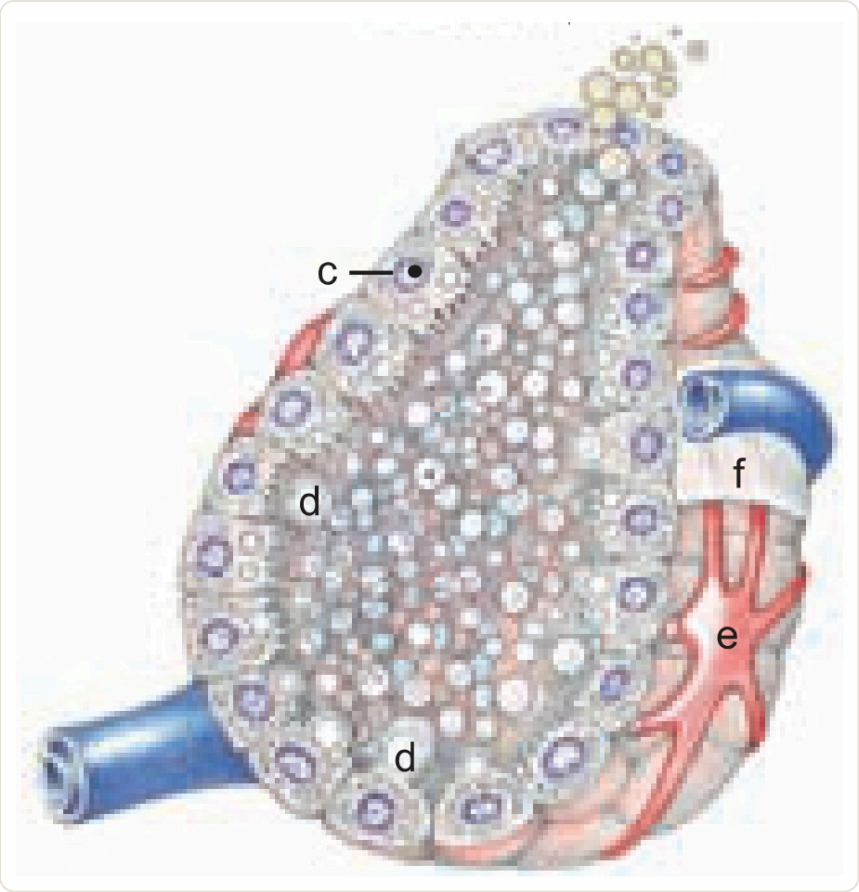

Fig 5 — The cell that makes the milk One alveolar cell at high magnification, with milk droplets leaving at the apex. *c* is the lactocyte itself, *d* the fat droplets, *e* the myoepithelial cell wrapped around the outside, and *f* the basement membrane it lies on. The droplets at the top are the apocrine mode caught in the act.

Image — Budras K-D, Habel RE, Mülling CKW, Greenough PR. Bovine Anatomy, 2nd extended ed. Schlütersche — folio 89, lower far-right plate: a lactocyte with its fat droplet, myoepithelial cell and basement membrane. Reproduced for educational reference.

The myoepithelial cell, and the reflex that uses it

A lactocyte cannot push milk anywhere. The pressure comes from the **myoepithelial cell**: an ectodermal derivative, like the gland itself, modified to carry contractile filaments so that it behaves like a smooth muscle cell. Myoepithelial cells lie between the secretory cells and the basal lamina, wrapped around each alveolus and continuing as a looser network around the smaller ducts. They carry **oxytocin receptors** on their surface, and when those are activated the cell contracts, the alveolar lumen narrows, and milk is forced out into the duct system. That is let-down, also called the milk ejection reflex.

The reflex arc is neurohormonal, and both halves of it are anatomy this page has already named or will name. Budras sets it out: the stimulus of suckling or of massaging the gland is carried by the **sensory nerves of the teat and udder skin** — the afferent limb, and the reason §11 is not an optional section — to the central nervous system. In the hypothalamic nuclei oxytocin is produced, and the afferent stimulus causes it to be released through the neurohypophysis into the blood, which carries it to the gland. There it finds the myoepithelial cells and milk is pressed into the ducts and the sinus.

The failure mode is worth knowing because it is anatomy's answer to a management problem. Under stress, adrenaline is secreted, and Budras states plainly that it **suppresses the action of oxytocin on the myoepithelial cells**. The milk is still there; the mechanism that moves it has been switched off.

06 The teat: the last centimetre

Everything above the teat is glandular tissue and storage. The teat is the part that has to open on demand, close reliably in between, survive being handled several times a day and keep bacteria out of a warm sac of milk. It is also the part of the animal a clinician physically touches most often, and it is built for those jobs in a way that is worth taking apart layer by layer.

The dimensions, and why the wall thickens at the bottom

The bovine teat is variable but most often cylindrical and **about 8 cm long**. Its wall is **generally about 6 mm thick**, and it *increases to about 1 cm at the lower end* — which is exactly where the papillary duct passes through it and where the closing mechanism lives. The thickening is not incidental; it is the muscle and elastic tissue of the sphincter making room for itself.

Three layers

LAYER	WHAT IT CONTAINS	WHAT IT IS FOR
Outer Skin	Dry, hairless skin, bound down tightly, and — on the teat — without skin glands	A working surface that will take repeated handling
Intermediate The functional layer	Smooth muscle and a dense venous plexus — a form of erectile tissue	Gives the teat its turgor; the reason teat injuries bleed persistently
Inner Mucosa	A mucous membrane thrown into folds; generally yellowish, but white in the papillary duct	Lines the teat sinus and the canal, and folds so the canal can close on itself

Of those three, the middle layer deserves emphasis, because of a practical consequence Budras states directly: the venous plexus in the teat wall forms an **erectile tissue**, and it is what *makes haemostasis difficult in injuries or surgery* of the teat. A structure that is designed to engorge does not stop bleeding readily.

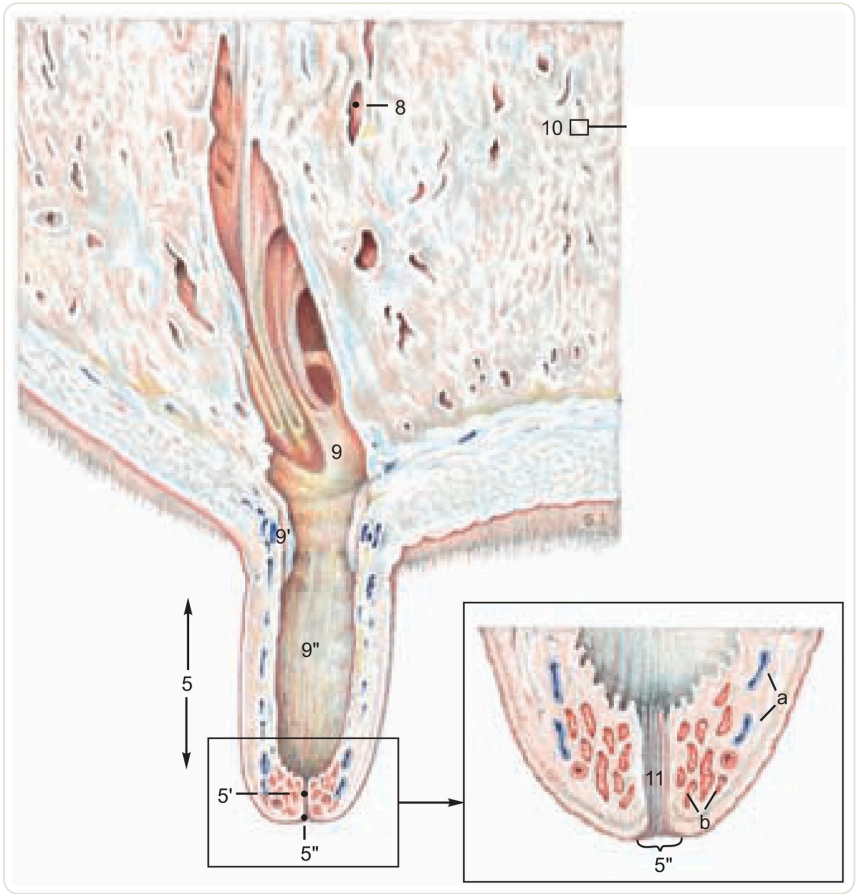

Fig 6 — The teat in section, and its orifice magnified The main panel runs from 8, a collecting duct in the gland tissue, down through 9 the gland sinus, 9' the annular fold, 9" the teat sinus, to 5' the teat canal and 5" the orifice; the bracket marked 5 spans the teat itself. The boxed lower end is magnified on the right: 11 the longitudinal folds of the canal, *a* the venous plexus of the teat wall, *b* the sphincter muscle, and 5" the orifice again. The small square marked 10 in the gland tissue is one lobule — the one magnified two figures earlier.

Image — Budras K-D, Habel RE, Mülling CKW, Greenough PR. Bovine Anatomy, 2nd extended ed. Schlütersche — folio 89, lower left plate: a sagittal section of the teat with a magnified detail of the orifice. Reproduced for educational reference.

The teat canal and its closing mechanisms

The **teat canal** or **papillary duct** is the last few millimetres, running from the teat sinus to the orifice at the apex. Three separate things keep it shut, and they are worth listing as three rather than as one:

- **A sphincter of smooth muscle**, reinforced by elastic tissue, around the canal. Dyce calls this the more effective means of closure.
- **A keratin plug.** The canal is lined by stratified squamous epithelium, and Budras describes it producing a plug of fatty desquamated cells that sits in the canal between milkings — an important factor in resistance to infection. Dyce puts the same fact the other way round: desquamation of the epithelium provides a bacteriostatic substance that helps occlude the passage.
- **Longitudinal mucosal folds.** The lining of the canal carries them, and they let the canal close on itself rather than having to be squeezed shut across an open tube.

> **Fürstenberg's rosette, and a hedge worth keeping**
>
> Where the teat sinus narrows into the teat canal, the mucosa is thrown into a ring of low radiating ridges. Budras names it: the proximal ends of the longitudinal folds form a radial structure called **Fürstenberg's rosette**. Dyce describes the same ridges — a pattern of low ridges in the white lining of the papillary duct, which when followed proximally radiate from the upper opening — and then adds, in a phrase worth quoting rather than smoothing away, that *it must be admitted that the arrangement is rarely as distinct as traditionally described*. Learn the rosette by name, and do not expect every specimen to show you one.

The teat end, and how much it varies

Not everything about a teat end is constant. Dyce illustrates four forms of the bovine teat extremity — funnel-shaped, dish-shaped, rounded and pointed — both in section and end on. The variation is normal anatomy and it is worth knowing simply because a reader who has only ever seen one drawing will not recognise the others.

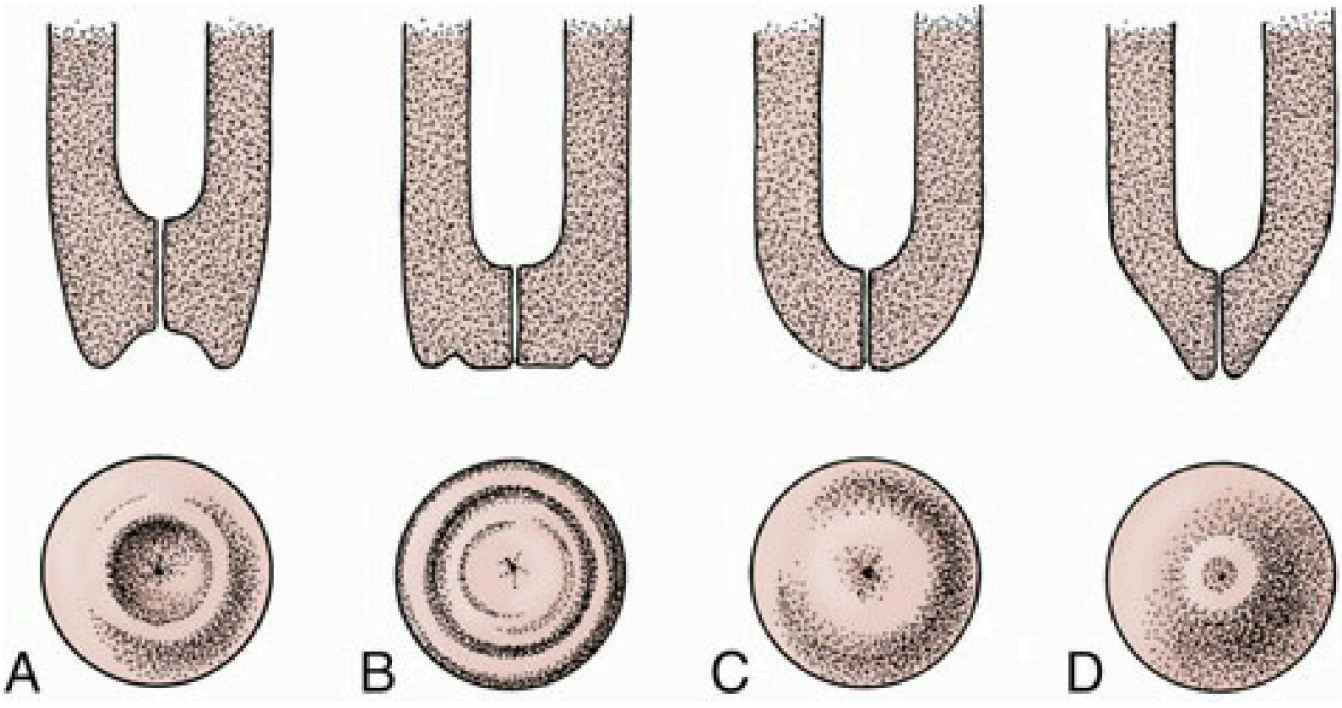

Fig 7 — Four normal teat ends The same structure, four normal shapes: (A) funnel shaped, (B) dish shaped, (C) rounded and (D) pointed. The upper row is a section through the end of the teat canal; the lower row is the same four teats seen end on, with the orifice at the centre of each.

Image — Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed. — Fig. 29.42, variations in the form of the bovine teat extremity. Reproduced for educational reference.

The teat in the other species

The bovine teat is the one described in detail everywhere, so the contrasts are easy to lose:

- **The mare** carries a single small cylindrical teat on each half, but the apex is perforated by **two, occasionally three, openings**, each leading through a short papillary duct to its own small lactiferous sinus. In the lactating mare the teat is larger and more conical.

- **The sow's** teats are elongated and cylindrical, each with two openings at the tip leading to independent gland units. Some project a little to the side, which matters because sows suckle lying down.
- **The bitch and the queen** have bare teats perforated by many fine openings — §8 has the counts — and in the virgin animal the teats are small and hidden by hair.
- **The goat's** teats are cylindrical in young animals but tend to become conical in older high-producing does and blend more smoothly into the gland.

07 How many, and where: the species pattern

Everything up to here has described one gland. This section is about all of them — how many a species has, where on the trunk they sit, and how the two facts are connected. It is the part of the subject that examiners like, because it cannot be reasoned out from first principles: either you know that a sow has seven pairs or you do not.

Three regions, and the ridge that decides them

Mammary glands are described by the region of the trunk they occupy: **thoracic**, **abdominal** and **inguinal**. §2 gave the reason the regions differ between species — the mammary ridge runs from axilla to groin in the embryo, and how much of it persists decides where the glands end up. Carnivores and the pig keep essentially the whole line, so their glands run from the chest to the groin. Ruminants and horses keep only the inguinal part, so their glands are consolidated there into an udder.

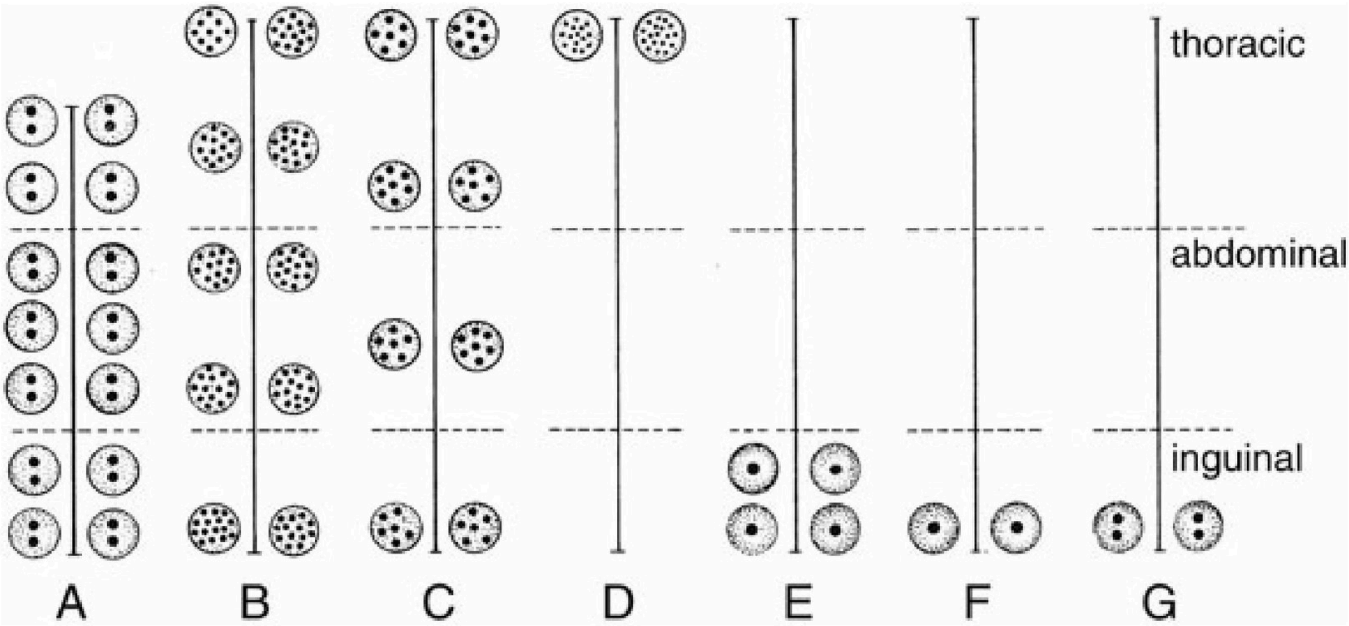

Fig 8 — Seven columns, three regions Each column is a species and each circle a teat, with the dots inside it marking the number of orifices on that teat. The two dashed lines divide the trunk into thoracic, abdominal and inguinal regions. (A) sow, (B) bitch, (C) cat, (D) woman, (E) cow, (F) ewe and she-goat, (G) mare. The woman is in the source plate and is kept here for a reason worth saying out loud: she is the reason a search for mammary gland anatomy returns human anatomy, and seeing her beside the cow is the fastest way to see what is different about the animals.

Image — Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed. — Fig. 10.32, the distribution of the mammary glands in certain mammals. Reproduced for educational reference.

The species table

Read the last column with the hedges attached. Dyce writes that dogs *generally* have five pairs and that the sow *almost invariably* has seven, and those words are doing real work: these are typical numbers, not fixed ones, and an animal with an extra pair is not abnormal.

SPECIES	GLANDS	WHERE	TEATS	OPENINGS PER TEAT
Cow	4 The four quarters	Inguinal — one udder	4, one per gland	**1**
Ewe	2	Inguinal — one udder	2	**1**

SPECIES	GLANDS	WHERE	TEATS	OPENINGS PER TEAT
Doe (goat)	2	Inguinal — one udder	2	**1**
Mare	2	Inguinal — one small udder	2	**2**, occasionally 3 Each opening has its own papillary duct and its own small lactiferous sinus
Sow	14 Almost invariably seven pairs	Thoracic to inguinal, in a double row	14	**2**
Bitch	10 Generally five pairs	Two thoracic pairs, two abdominal, one inguinal	10	**10 or 12**
Queen (cat)	8 Four pairs	Thoracic to inguinal	8	**4 to 8**

Fig 9 — The same six species, as a card Gland number, region and openings per teat for the six domestic species most often asked about, in the form that fits on one screen. Every figure on it is quoted from the chapter named in the species table.

Diagram — Vet-eBooks.com, drawn for this guide. Data from Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed., ch. 10 and ch. 29.

What the pattern is actually telling you

Three things are worth extracting from that table rather than left in it.

- **Gland number tracks litter size, not body size.** The sow with fourteen glands is not a large cow; she is an animal that raises ten or more young at once. The cow, the mare, the ewe and the doe raise one or two and have two or four glands.
- **Position tracks how the young feed.** The species whose young lie in a row along the mother — the sow, the bitch, the queen — have glands in a row along the mother. Dyce notes that in the bitch the often staggered pattern of the two chains makes all the teats equally accessible when she suckles lying on her side, and that the sow's habit of suckling in lateral recumbency means teats that project sideways may not be reached at all.
- **Duct count per teat runs the other way from gland count.** The cow has the most glandular tissue per gland and the fewest openings per teat — exactly one. The bitch has ten or twelve. §8 explains why, and the explanation is a single developmental fact.

Why this subject's search results are human

It is worth naming, because it changes how a student should read what a general search returns. Search for mammary gland anatomy and the first page is human: the nipple in the fourth intercostal space, fifteen to twenty lactiferous ducts opening on it, the tubercles of Montgomery, the suspensory ligaments of Cooper. Not one of those terms belongs to any animal on this page. The woman in the comparative plate has **one pair of thoracic glands**, which is a pattern no domestic species shares. Take the vocabulary from a veterinary source or it will not match the specimen in front of you.

The udder, species by species

Four species have an udder in the strict sense, and they are not built alike:

- **The cow.** Four glands in one mass, divided into quarters, each with a principal teat. The right and left halves are separated by the intermammary groove and by real medial laminae; the fore and hind quarters of one side are not separated by anything except their own duct systems.
- **The mare.** Two glands in a rather small udder, tucked up between the thighs and, as Dyce puts it, concealed from casual inspection by the thigh. A prominent external groove shows its formation from right and left halves. It is very small in young virgin animals.
- **The doe.** Two glands. In milk goats the udder is large in relation to body size, deep and conical.
- **The ewe.** Two glands, smaller and more hemispherical than the goat's, though breeds used for cheese production incline towards the caprine form. Budras and Dyce agree that the two glands are more distinctly demarcated externally in the goat than in the sheep.

08 How many holes in a teat, and why

§7 gave the numbers. This section gives the cause, and it is a single fact from the embryo that explains the whole column at once. The two sections belong together and should be read together.

One sprout, one duct system, one hole

Go back to the mammary bud. From each bud, one or more **epidermal sprouts** grow proximally from the tip of the developing teat into the connective tissue. Dyce states the rule in a single sentence: the mammary gland arising from **only one sprout** has a single duct system leading to a single orifice on the tip of the teat. And where more than one sprout appears, *the number of sprouts results in a corresponding number of separate duct systems*, each with its own associated glandular mass and its own separate orifice.

So the chain is fixed and runs in one direction:

The chain that fixes the orifice count

Sprouts on the mammary bud → that many **separate duct systems** → that many **lactiferous sinuses** → that many **papillary ducts** → that many **orifices on the tip of the teat**. The number is settled before birth and every later count follows from it. That is why the orifice count is a species character and not a variable: one sprout in the cow, two in the mare and the sow, ten or twelve in the dog.

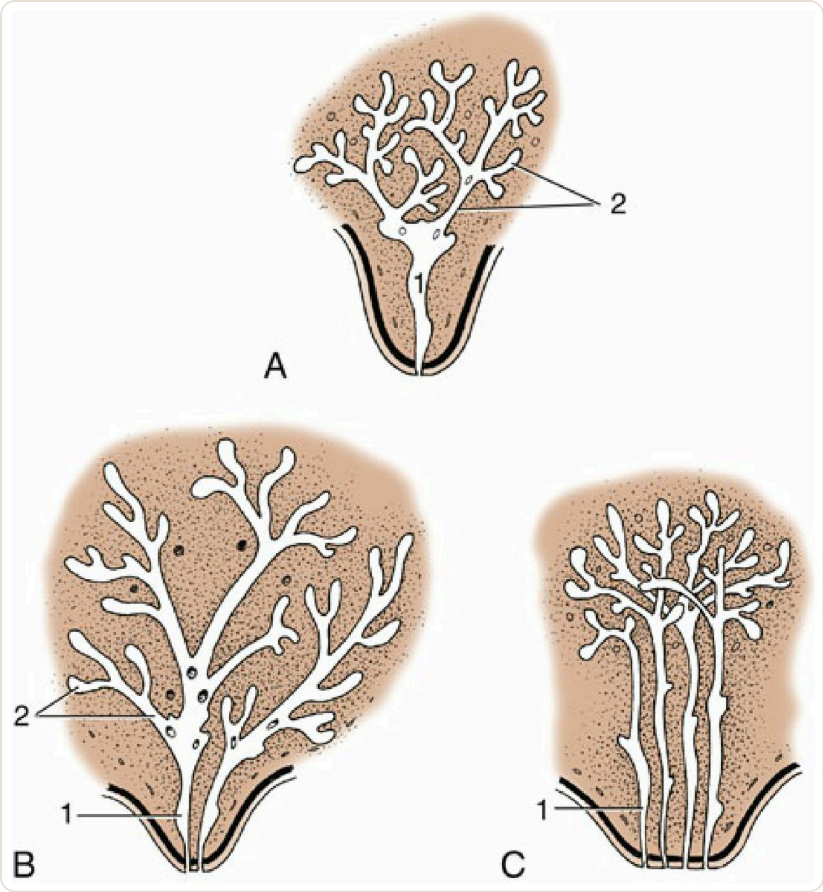

Fig 10 — The sprouts that decide the count Duct systems growing proximally from the tip of the fetal teat, drawn for three groups: (A) cow and goat, (B) mare and sow, (C) bitch and cat — where only four of the primary sprouts are drawn, for clarity. 1 is the primary sprout, which becomes the lactiferous sinus; 2 the secondary and tertiary sprouts, which become the ducts. Count the stems entering each teat at the bottom of each panel and you have counted the orifices that species will have.

Image — Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed. — Fig. 10.31, developing duct systems growing proximally from the tip of the fetal teat. Reproduced for educational reference.

Reading the species down that chain

Every entry in the last column of the species table is now derivable rather than memorised:

- **Cow, ewe and doe — one sprout.** One duct system, one lactiferous sinus, one papillary duct, one orifice. Budras states the consequence explicitly and points at the contrast: in the cow, in contrast to the bitch and the mare, each mammary gland contains only one duct system and its associated glandular tissue.
- **Mare and sow — two sprouts** (occasionally three in the mare). Two independent gland units share one teat. In the mare each of the two apical openings leads through its own short papillary duct to **its own small lactiferous sinus**, spread between the teat and the gland mass, with its own independent set of lactiferous ducts. Dyce adds the caution that on the bench this independence cannot actually be demonstrated: the tissues of the individual glands of each side interdigitate.
- **Bitch and queen — many sprouts.** The bitch's teat is perforated by **10 or 12** fine openings and the cat's by **4 to 8**. Each of those is the outlet of a separate small lactiferous sinus served by its own duct system, which is the general case Dyce describes for species in which each gland contains several small lactiferous sinuses, each served by a separate duct system and each opening independently.

Notice what this does to the phrase "the teat sinus". In the cow it is a definite article: there is one, and it holds a substantial volume. In the bitch there are ten or twelve tiny ones. The bovine account of the teat in §6 is not a general account with the numbers changed; it is the account of a species that took the one-sprout route and then made the single duct system very large.

Supernumerary teats, and the two words for them

The same developmental fact explains the commonest abnormality of the gland. More buds appear on the ridge than survive; most of the extras regress, and some do not. What is left is an extra teat, an extra gland, or both, sitting somewhere on the line the ridge used to occupy.

- **Hyperthelia** is supernumerary *teats* — from the Greek *thele*, nipple.
- **Hypermastia** is supernumerary *glands*.

They are common. Dyce calls accessory teats in the cow *very common*, and Budras says they occur and are not rare; in goats Dyce notes they are *not uncommon*. They may be independent or attached to a better developed gland, and they may be sometimes associated with functional glandular tissue. In the cow they usually sit caudal to the normal teats, but they may be between them or cranial to them. Where they sit on a main teat rather than beside it they interfere with milking, which is why they are often removed from the udders of cows and goats.

The bull has them too, and they are not an abnormality: rudimentary teats occur cranial to the scrotum. §13 comes back to that.

09 What holds it up

A high-yielding dairy cow carries an organ under her abdomen that may weigh a great deal more than the tissue attaching it, and it hangs from a body wall with no bone anywhere near it. The answer to "why does it not fall off" is the **suspensory apparatus**, and it is one of the more elegant pieces of design in the domestic animals: two sheets with different mechanical properties, doing two different jobs, and failing in a characteristic way when they fail.

Two laminae, two materials

The udder is suspended by strong sheets of fascia that surround and enclose the gland substance and are continuous with the connective-tissue framework running through the whole organ. Dyce is careful to say that the investment is actually continuous over each half, and that describing medial and lateral laminae as separate formations is a convention. It is a useful convention, because the two regions genuinely differ in what they are made of.

PART	WHERE IT COMES FROM	WHAT IT IS MADE OF	WHAT IT DOES
Medial laminae The paired paramedian suspensory ligament	Mainly from the tunica flava — the yellow abdominal tunic — on the outer surface of the prepubic tendon, and in small part from the symphyseal tendon	**Largely elastic tissue**	Separates the right and left halves and carries most of the give; stretches under load
Lateral laminae	From the lateral crus of the superficial inguinal ring and, behind that, from the medial femoral fascia and the symphyseal tendon Dyce calls it the **external** crus and Budras the **lateral** crus. They are the same structure	**Dense regular collagenous tissue**	Passes over the outer surface of each half; takes the weight without stretching
Suspensory lamellae	Detached from both laminae as they run ventrally	Thin sheets of the same fascia	Penetrate the gland and divide the parenchyma into curved, overlapping lobes; carry the vessels and nerves
Symphyseal tendon	The pelvic symphysis	Tendon	The caudal bony anchorage; contributes to both laminae
Tunica flava Yellow abdominal tunic	The elastic deep fascia of the abdominal wall	Elastic	The cranial anchorage, and the origin of the medial laminae

From both laminae, thin **suspensory lamellae** pass into the gland substance, dividing the parenchyma into curved, overlapping lobes and carrying the vessels and nerves with them. Dyce notes that both laminae thin as they are followed ventrally, and that this is precisely because they are detaching those leaves as they go. The apparatus does not hold the udder up from the outside; it is threaded all the way through it.

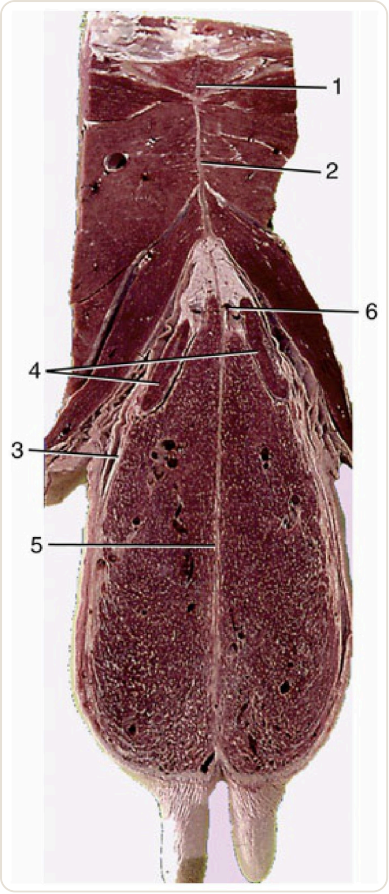

Fig 11 — The apparatus, in transverse section A transverse section through the pelvic floor and the caudal quarters. 1 is the pelvic symphysis and 2 the symphyseal tendon hanging from it; 3 the lateral suspensory laminae passing down the outside of each half; 5 the medial suspensory laminae meeting in the midline; 4 the mammary — superficial inguinal — lymph node, lying deep to the lateral lamina, which is where §11 says to look for it; and 6 a tributary of the external pudendal vein.

Image — Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed. — Fig. 29.40, a transverse section of the pelvic floor and the caudal quarters of the udder. Reproduced for educational reference.

What the difference in material predicts

This is the part worth understanding rather than memorising, because it explains something a student can see in any dairy herd.

The medial laminae are **elastic**. The lateral laminae are **dense collagenous** tissue, which is strong and does not stretch. When the udder fills, its weight stretches the suspensory apparatus, and it stretches the elastic part more than the fibrous part. Two visible consequences follow, and both books name them:

- **The medial part of a heavily laden udder sags.** Dyce attributes the sagging directly to the different natures of the two laminae.
- **The teats of a tightly filled udder point outwards and forwards.** Budras traces it through: the elastic medial laminae stretch more than the lateral, the floor of the udder drops between them, and the teats are carried laterally and cranially.

Dyce records the endpoint of that process without embellishment, and this page will do the same — the anatomy, and nothing attached to it: ever-increasing demands for milk production place a heavy and sometimes unsustainable burden on the suspensory apparatus, *which occasionally ruptures — a disastrous outcome*.

The plane between the halves

One consequence of the medial laminae being paired and paramedian rather than single is surgical, and it is anatomy rather than technique. Because there are two of them, right and left, there is a genuine cleavage plane between the two halves of the udder. Budras notes that the median separation can be demonstrated by blunt dissection between the medial laminae from their caudal borders, and that the separate medial laminae are what make it possible to amputate one lateral half of the udder. Dyce says the same of the mare: the medial ligaments provide a cleavage plane between the apposed surfaces of the udder halves.

The mare's version

The mare has the same design at a smaller scale. Dyce describes her suspensory apparatus as much less developed but built the same way — medial elastic and lateral fibrous ligaments, which together encapsulate the udder and supply the lamellae that support the parenchyma.

10 Blood, and where the milk vein comes from

Support and supply are the two halves of "how does it stay there and work". This section is the supply, and it opens with the number that makes sense of everything after it.

How much blood a litre of milk costs

Budras gives the figure that explains why the vessels of the udder are the size they are: **up to 600 litres of blood must flow through the udder to produce one litre of milk**. It is an estimate and the book presents it as one — but the order of magnitude is the point. An organ with that throughput needs arteries and veins out of all proportion to its size, and it gets them; Budras notes that they are remarkable for their large calibre and have been given extra names because of it.

The arteries

The main supply to the bovine udder continues the **external pudendal artery**. Two things about it are worth carrying: its size and its route.

- **Size.** Dyce records a diameter that *may exceed 15 mm* where it passes through the inguinal canal — a vessel the width of a little finger, supplying a skin gland.
- **Route.** It passes through the inguinal canal accompanied by a satellite vein, by lymphatics and by nerves. That bundle is the reason the inguinal canal keeps appearing in this article: it is the door through which everything the udder needs arrives.

On reaching the base of the udder the artery divides into two divergent branches, one running cranially and one caudally — the **cranial** and **caudal mammary arteries** — both partly or wholly embedded in the gland substance. The caudal mammary branch anastomoses with a division of the ventral perineal artery; Dyce notes that this restricts the perineal contribution to the mammary lymph nodes and a limited portion of the hindquarter, so it is a real anastomosis but not a major alternative supply.

VESSEL	WHERE IT COMES FROM	WHAT IT SUPPLIES
External pudendal artery	Through the inguinal canal, with a satellite vein, lymphatics and nerves May exceed 15 mm in diameter in the canal	The main supply to the whole udder
Cranial mammary artery	One of the two divergent branches at the base of the udder	The forequarter, largely embedded in the gland substance
Caudal mammary artery	The other divergent branch	The hindquarter; anastomoses with a division of the ventral perineal artery
Ventral perineal artery Through its mammary branch and the ventral labial vessels	The perineum, from behind	The mammary lymph nodes and a limited part of the hindquarter — a real but restricted contribution

The veins, and the ring

Dyce introduces the venous side by saying the pattern is complicated, and it is, but it resolves into three statements.

First, there is a ring. A venous ring lies above the udder, formed by paired veins connected across the midline by transverse vessels. The right and left cranial mammary veins anastomose on the cranial border of the udder and the caudal mammary veins do the same behind, and between them they close the ring around the base. Many of the udder's veins simply join it.

Second, there are two exits. Blood leaves the ring by the **external pudendal veins**, which pass back through the inguinal canals, and by the **subcutaneous abdominal veins** — the milk veins — which run forward. The milk veins pursue very flexuous subcutaneous courses over the abdominal floor and then disappear through palpable openings in the body wall, the **milk wells**, to discharge into the **internal thoracic veins**.

Third, the names double up, which is where most confusion about this region comes from, so it is worth setting out plainly:

- The **cranial mammary vein** is also the **caudal superficial epigastric vein**.
- The **subcutaneous abdominal vein** — the visible milk vein — is also the **cranial superficial epigastric vein**.
- The **milk well** is the point where it perforates the abdominal wall in the xiphoid region to reach the internal thoracic vein.

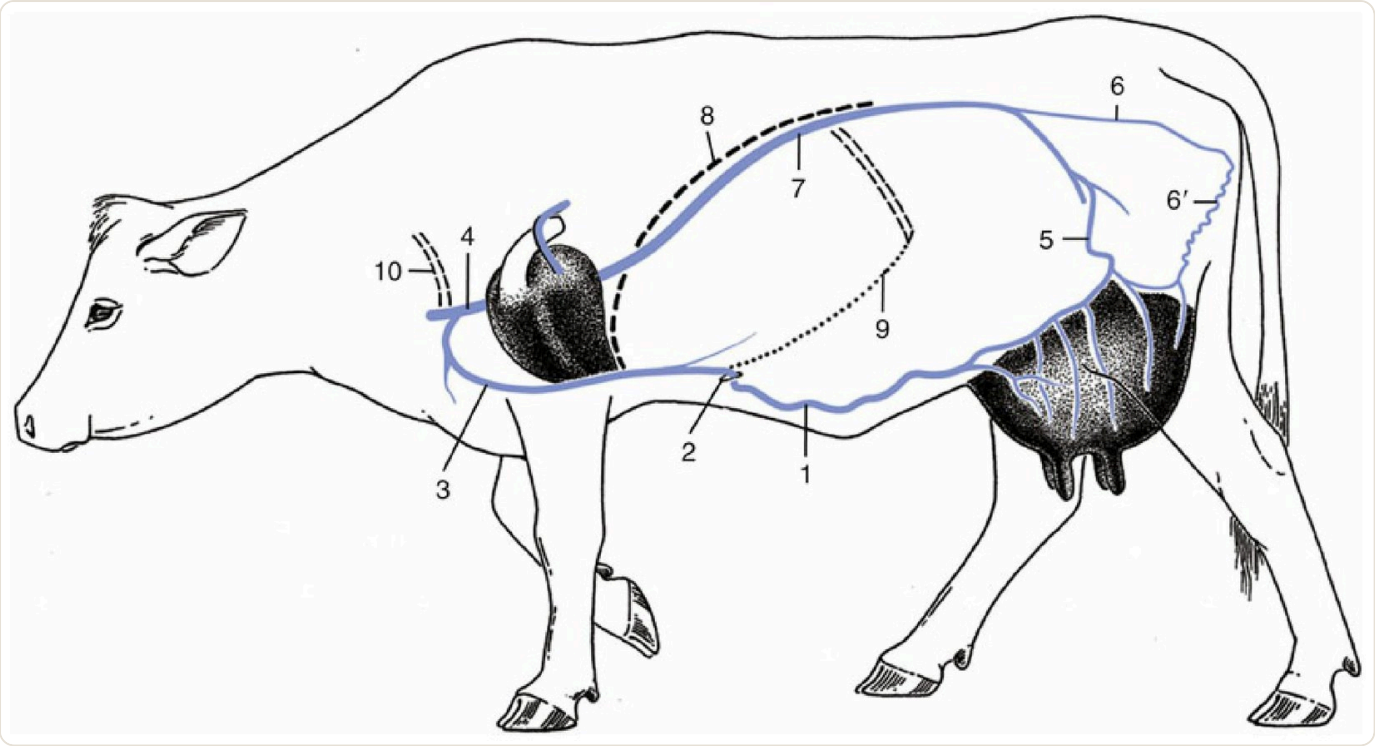

Fig 12 — Where the milk vein goes The route drawn on the whole animal. 1 is the subcutaneous abdominal — "milk" — vein running forward under the skin of the abdominal floor; 2 the "milk well" where it dives through the body wall; 3 the internal thoracic vein it joins; 4 the cranial vena cava; 5 the external pudendal vein, the other exit, passing back through the inguinal canal; 6 the internal pudendal vein and 6' the ventral labial vein; 7 the caudal vena cava; and 8, 9 and 10 the diaphragm, costal arch and first rib for orientation. Both exits are drawn, and the ring above the udder connects them.

Where the milk vein comes from

The milk vein of a dairy cow is not a vein that grew. It is **two territories whose valves failed**, and the sequence is worth telling as a sequence because it is one of the few pieces of gross anatomy that is unambiguously a developmental event a student can watch happen.

How a milk vein is made

In the calf and the heifer, the region drained by the cranial superficial epigastric vein is *separate* from the region drained by the caudal superficial epigastric vein. Valves in the cranial vessel direct blood cranially; valves in the caudal vessel direct it caudally. Two territories, draining in opposite directions, with a watershed between them. **During the first pregnancy,** blood flow through the enlarging udder increases sharply. The veins distend, the distension makes the valves incompetent, and the two drainage regions unite into one continuous channel. **The result** is a single flexuous vessel in which blood can flow in either direction — and which is large enough to be seen bulging under the skin. That is the milk vein.

Dyce adds the reason this arrangement is worth having rather than merely tolerating: the significance of the mature pattern lies in its assurance of effective venous drainage should some channels be occluded in the recumbent cow. A cow lying on one side has compressed one route; the united channel means the other still works.

And one caution, stated as anatomy. The milk vein is sometimes used for intravenous injection or blood sampling. Dyce's verdict is that *it is not a wise choice*: its varicosed structure predisposes it to potentially troublesome leakage.

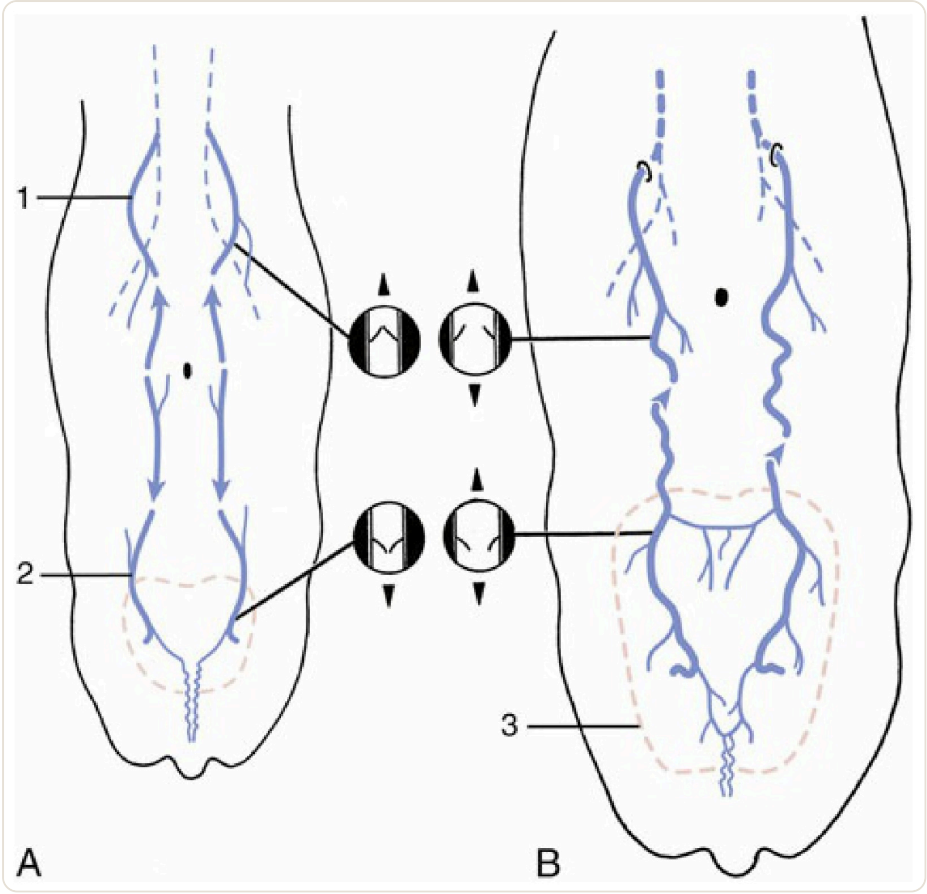

Fig 13 — The two territories, before and after Schematic dorsal views. (A) The calf and heifer: 1 is the cranial superficial epigastric vein and 2 the caudal, draining in opposite directions — the four circular insets show the valves, with the arrows beside them giving the direction each set permits. (B) After the first pregnancy: 3 marks the enlarged udder whose blood flow distended the veins, the valves have become incompetent, and the two territories have united into one channel that will carry blood either way.

Image — Singh B (ed). Dyce, Sack and Wensing's Textbook of Veterinary Anatomy, 5th ed. — Fig. 29.45, the development of the subcutaneous abdominal veins. Reproduced for educational reference.

The other species, briefly

- **The mare.** Supply from the external pudendal artery; the principal venous return is by the corresponding vein, which — unlike the cow's — does not follow the usual course through the inguinal canal. And as in the cow, Dyce records that a subcutaneous venous connection with a superficial vein of the thoracic wall develops as an alternative drainage route during the first pregnancy: the mare grows a milk vein too.
- **The bitch and the queen.** The lateral thoracic, internal thoracic and external pudendal arteries are the major sources, with satellite veins. Both arteries and veins anastomose freely and form plexuses which *may cross the midline* — a fact worth holding on to for the next section. The external pudendal and genitofemoral route through the canine inguinal canal is followed in more detail in our guide to the dog's abdominal anatomy for surgery.
- **The sow.** Supplied by local vessels rather than one dominant trunk: the internal thoracic and the cranial and caudal superficial epigastric arteries, with satellite venous drainage. A row of fourteen glands from chest to groin cannot be fed through one inguinal canal.

11 Lymph and nerves

These two follow the vessels through the same door, and between them they are the part of the mammary anatomy that differs most between species. They are also the part most likely to be asked about in a practical, because both end in something you can put a hand on.

Lymph in the cow

The teats and the gland substance are permeated by a rich lymphatic plexus, from which larger vessels emerge and run to the **mammary lymph nodes** — also called the **superficial inguinal** nodes — sitting above the caudal part of the udder, on the surface applied to the body wall.

Three practical details go with them:

- **They can be palpated.** Budras gives the landmark: between the thighs, about 6 cm from the skin, at the caudal attachment of the udder. Dyce says the larger of them may be reached on deep palpation from behind, and that they lie **deep to the lateral lamina** of the suspensory apparatus — which is why Figure 11 labels one.
- **The big lymphatics are visible, and can be told from veins by their direction.** Dyce notes that many of the large lymph vessels show through the skin and run **caudodorsally**, which distinguishes them readily from the subcutaneous veins running **craniodorsally**. That is a genuinely useful discrimination and it costs nothing to learn.
- **The next node up can be reached per rectum.** Efferent flow is to the **deep inguinal** node — Budras calls it the iliofemoral node — lying in the angle between the deep circumflex and external iliac arteries. Dyce records that it may be palpated per rectum.

> **How many mammary nodes? The books differ**
>
> Dyce writes that the mammary lymph nodes are **generally two on each side**, one large and one much smaller. Budras writes that lymph is conducted to **one to three superficial inguinal nodes**, and adds that small intramammary nodes may also be present. Both are describing the same region and neither is a misprint; the count is genuinely variable, and the two books have drawn the boundary of "the node" differently. If a number is wanted, say **one to three, usually two**, and name the source. Do not present either figure as the settled one.

Lymph in the other species

This is where the species diverge most, and the reason is the one from §7: a chain of glands running from the chest to the groin cannot all drain backwards.

SPECIES	WHERE THE LYMPH GOES	NOTE
Cow	All quarters → mammary (superficial inguinal) nodes → deep inguinal (iliofemoral) node	The whole udder is inguinal, so it all drains one way
Sow	First two — or three — pairs → **ventral superficial cervical** nodes; the remainder → superficial inguinal nodes	A chain from chest to groin drains in two directions, forward and back
Bitch and queen	Cranial glands → axillary and accessory axillary nodes, and the sternal node; caudal glands → superficial inguinal nodes	Dyce: the pathways are **erratic**, and some lymph may cross the midline. In the cat it is said that the vessels do not cross the midline nor penetrate the thoracic wall
Mare	Mammary (superficial inguinal) nodes	As in the cow, and for the same reason

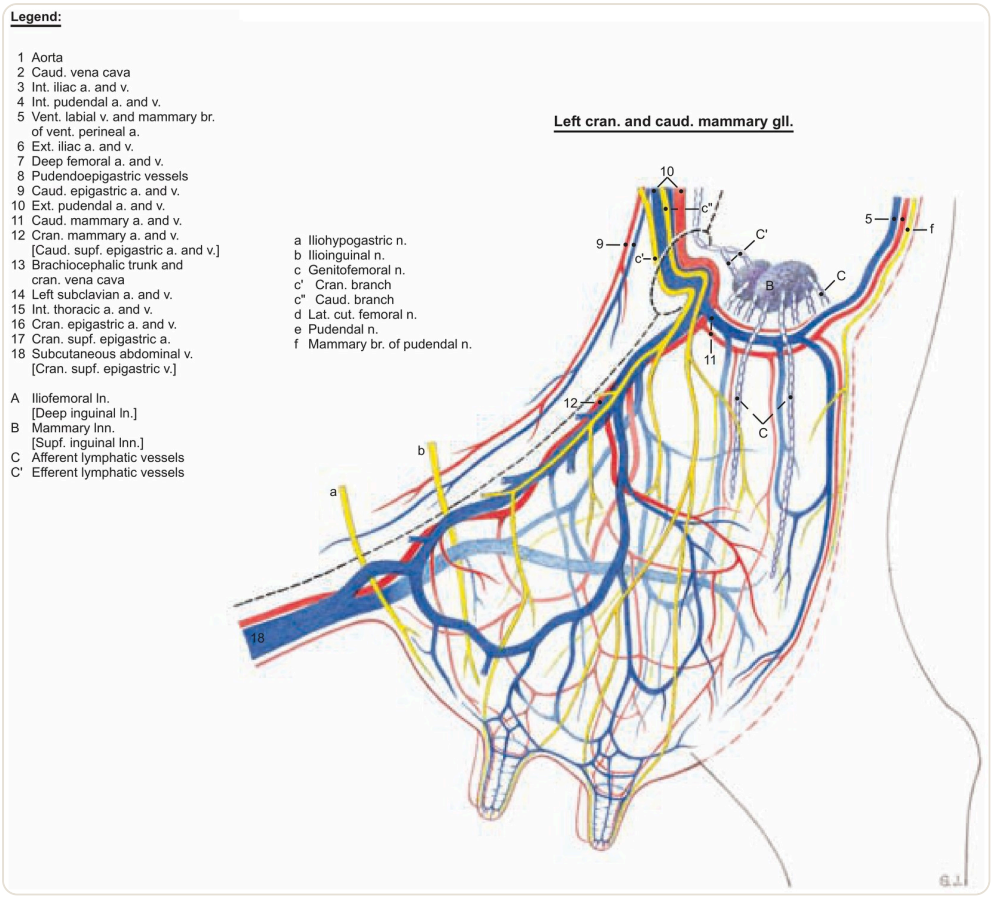

Fig 14 — Vessels, lymph and nerves on one plate The left half of a bovine udder with everything that reaches it, and the book's own legend beside it — 18 numbered vessels, four lymphatic symbols and six nerves. Work from the legend outwards: 10 the external pudendal artery and vein entering through the inguinal canal, dividing into 12 cranial and 11 caudal mammary vessels; 18 the subcutaneous abdominal vein leaving to the left; B the mammary lymph nodes with C the afferent and C' the efferent lymphatics; and *a* to *f* the nerves, of which *c*, the genitofemoral, supplies both quarters and the gland substance.

Image — Budras K-D, Habel RE, Mülling CKW, Greenough PR. Bovine Anatomy, 2nd extended ed. Schlütersche — folio 91, lower plate and its legend: arteries, veins, lymph nodes and nerves of the left mammary glands. Reproduced for educational reference.

Nerves

Dyce opens the bovine account by calling the cutaneous innervation of the udder *inconveniently diffuse*, which is a fair warning: there is no single mammary nerve. He names three sources for the *skin*: ventral branches of the first two lumbar nerves, the genitofemoral nerve, and mammary branches of the pudendal nerve. Then he names one for the *inside*. The gland substance and the deeper tissues of the teat wall are supplied by the **genitofemoral nerve alone**, which reaches the udder through the inguinal canal.

Budras divides the same supply by region rather than by depth, which is the more useful way to hold it for a practical:

REGION	NERVES	FROM
Skin and teats of the forequarters, and the cranial part of the base	Iliohypogastric nerve, ilioinguinal nerve, and the **cranial branch** of the genitofemoral nerve	The first two lumbar nerves and the lumbar plexus
Skin and teats of the hindquarters	**Caudal branch** of the genitofemoral nerve, and the mammary branch of the pudendal nerve	The lumbar plexus and the pudendal nerve
Gland substance and the deep tissue of the teat wall	**Genitofemoral nerve alone** — both branches pass through the inguinal canal into the body of the udder	The lumbar plexus, entering with the vessels

Two things are worth saying about that table. The first is that the **genitofemoral nerve** appears in every row: its cranial branch to the forequarters, its caudal branch to the hindquarters, and by itself to the gland substance and the deep teat wall. If one nerve had to be named for the udder, it is that one. The second is that this sensory supply is not merely sensation. Budras states it directly: the sensory innervation of the teats and the skin of the udder is the **afferent pathway of the neurohormonal reflex arc** that is essential for the initiation and maintenance of milk expulsion. §5 described the efferent half. This is the half that starts it.

In the mare, Dyce divides the cutaneous supply between the nerves of the flank and a descending mammary branch of the pudendal nerve, giving cord segments L2–L4 and S2–S4; the substance of the gland is supplied by the genitofemoral nerve, L3–L4. The same pattern, in the same order.

12 From ridge to lactation, and back

Few organs are built, taken most of the way apart and built again, repeatedly, in one animal's life. The endometrium does it every cycle; the mammary gland does it once per lactation, and on a scale that changes the shape of the animal. It is worth walking through once as a sequence, because half the anatomy above only makes sense at a particular point in it.

Before birth

The ridge appears in the embryo of *both sexes*, on the ventrolateral body wall between the primordia of the thoracic and pelvic limbs. Epithelial sprouts grow down from it into the mesenchyme to form the mammary buds, in the location and number characteristic of the species. In ruminants and the horse the teat then forms as a proliferation teat, by growth of the areolar tissue around the sprout, with the ring of skin around the bud taken up into it.

By full term the gland is recognisable but nearly empty of the thing it is for. Dyce describes it: short but well-formed teats, small sinuses, and the first branches of the duct systems. **The bulk of the udder at birth is fat.**

Calf to heifer: two different kinds of growth

What happens next is the piece most often got wrong, because there are two phases and only the second one is what a reader would call "development".

- **Growth that keeps pace with the body.** For the first few months, growth of the udder keeps pace with the general growth of the animal and is, in Dyce's words, *entirely due to deposition of fat*. Nothing glandular is happening.
- **Growth that outruns the body.** Thereafter — and, importantly, *commencing well before puberty* — growth quickens and the duct system and gland tissue develop rapidly. Dyce attributes this to the cyclical production of oestrogen, on the evidence that spurts of activity occur directly before ovulation. Budras describes the same phase from the other end: as ovarian follicles ripen in the young heifer and blood oestrogen rises, connective and adipose tissue increase and the epithelial buds proliferate, dividing repeatedly to produce the small collecting ducts.

The gland then **stops and waits**. Budras: the mammary gland primordia rest in this stage of proliferation until the first pregnancy.

The first pregnancy

A well-developed duct system is present by the time a heifer first conceives, and pregnancy adds the rest in two halves. Additional growth of the **ducts** predominates in the first months; the **secretory tissue** grows in the second half, and the space-occupying adipose tissue is displaced as it does. Towards the end of gestation — about 280 days in the cow — a lumen develops in the still partly solid glandular end-pieces under the influence of progesterone and oestrogen, and under the influence of **prolactin** the lactocytes begin to secrete. That step has its own name: **lactogenesis**.

Lactation can begin a few days or a few hours before parturition, and Budras notes the practical sign: the first drops of milk on the end of a teat are taken as an indication of impending birth.

Two other things happen during that first pregnancy, and both have already been described in their own sections: the venous valves fail and the milk vein forms (§10), and the suspensory apparatus takes load for the first time (§9).

STAGE	WHAT IS HAPPENING	DRIVEN BY
Embryo	Mammary ridge, then buds; teat forms by proliferation in ruminants and the horse	Development, in both sexes
Birth	Short teats, small sinuses, first duct branches. The bulk of the organ is fat	—
Calf, first months	Growth keeps pace with the body and is entirely fat deposition	General growth
Before puberty onwards	Growth outruns the body; ducts and gland tissue develop rapidly, then rest Spurts occur directly before ovulation	Cyclical oestrogen
First pregnancy, first half	Duct growth predominates; the milk vein forms	Pregnancy
First pregnancy, second half	Secretory tissue grows and displaces fat; lumina open in the end-pieces	Progesterone and oestrogen

STAGE	WHAT IS HAPPENING	DRIVEN BY
Around parturition	Lactogenesis begins; colostrum for about five days	**Prolactin**
Lactation	Maintained in the quarters that are emptied; unused quarters involute	Corticotropin, TSH, somatotropin — and regular milking
Involution	Secretory cells degenerate; glandular tissue is replaced by fat and connective tissue	Weaning, or a deliberate dry period of about 60 days
After	Smaller, but never **quite** back to the pre-lactation size; a little larger after each pregnancy	—

Lactation, and what maintains it

Growth in late pregnancy depends on prolactin and growth hormone of hypophyseal origin, in addition to progesterone and oestrogen. Secretion is later maintained by corticotropin, thyroid-stimulating hormone and somatotropin — and by something much more mechanical: **regular milking**. Dyce explains the link: because the act of milking itself stimulates the release of prolactin, oxytocin and corticotropin, more frequent milking, within limits, increases the yield.

The same principle decides which parts of the gland stay in production. Budras states it at the level of the quarter: after birth, milk secretion is maintained only in the quarters the suckling uses, and the unused quarters rapidly undergo involution. A quarter that is not emptied stops being a quarter.

Involution, and the part that does not come back

When the young are weaned — or, in dairy practice, when the ration is reduced and milking tapered to give a dry period of about 60 days after a lactation of about ten months — involution sets in. The sequence is the reverse of the build:

- The secretory cells in the alveoli and the alveolar lactiferous ducts **degenerate**.
- The parenchyma regresses and the **glandular tissue is replaced by fat and connective tissue**. Budras notes why this matters at the animal's side: it is important for the clinical evaluation of the consistency of individual quarters — a quarter that feels different may be a quarter at a different stage.
- The connective tissues now form the bulk of the organ, and the size of the udder decreases.

But it does not go all the way back. Both books say so independently, and it is the detail worth finishing the section on: the gland **never quite reverts to its pre-lactation size**, and it grows a little more with each pregnancy. Budras puts it as never returning to the small size of an udder that has not yet produced milk. An udder carries its own history.

13 Males, extra teats, and what varies

The last section is the exceptions, and it is here rather than earlier for a practical reason: these are the things that turn up in front of you and are not in the standard drawing, and they are where marks are actually lost.

Males have them, and it is not an abnormality

The mammary ridge forms in the embryo of both sexes, so mammary buds form in male embryos too. They persist, and they give rise to rudimentary teats. Where those teats end up is species-specific and is the sort of question that has a clean answer:

- **Carnivores and the pig** — on the ventral surface of the trunk, in the same positions as the female's.
- **Ruminants** — on the **cranial surface of the scrotum**. Budras puts it as rudimentary teats occurring in the bull cranial to the scrotum.
- **Horses** — less common, but they occasionally appear beside the prepuce.

Not every mammal keeps them. Dyce records that in certain species such as rats the male glands regress completely, which is a useful reminder that "males have rudimentary teats" is a statement about particular species and not a mammalian universal.

Budras adds what happens if the male gland is given the female signal: normally the male udder remains at the calf stage throughout life, but during puberty some bull calves can undergo a further temporary growth of the mammary glands under the influence of an elevated level of oestrogen, exactly as is natural in the female. The tissue is not different; the hormonal environment is.

Extra teats and extra glands

§8 gave the two words — **hyperthelia** for extra teats and **hypermastia** for extra glands — and the developmental reason: buds that should have regressed did not. What is worth adding here is where they turn up and what actually follows from them.

- **Position.** In the cow they are usually caudal to the normal teats, but may lie between them or cranial to them.
- **Attachment.** They may be independent, or attached to a better developed gland.
- **Function.** They are sometimes associated with functional glandular tissue — an accessory teat is not necessarily a blind one.
- **Frequency.** Very common in the cow; not uncommon in goats.
- **Consequence.** The anatomical consequence, and the only one this page makes, is mechanical: a teat sitting on a main teat interferes with milking, which is why such teats are often removed from the udders of cows and goats.

What else varies, and is still normal

Four kinds of variation have appeared in passing above. They are collected here because a reader who has only seen the textbook drawing may mistake any of them for a lesion.

- **Teat-end shape.** Funnel, dish, rounded and pointed are all normal bovine forms (§6).
- **The prominence of the annular fold.** It varies, and Dyce records that occasionally it is pronounced enough to impede milk flow (§4).
- **Fürstenberg's rosette.** Named in every textbook, and *rarely as distinct as traditionally described* in an actual specimen (§6).
- **The number of mammary lymph nodes.** One to three, usually two, and the two standard books give different figures (§11).

And the small ruminants, which are not just small cows

The goat and the sheep have the same two-gland plan and differ from each other in ways that are easy to see and easy to be asked about. In the goat the two glands are more distinctly demarcated externally; in the sheep, less so. In milk goats the udder is large in relation to body size, deep and conical; in ewes it is smaller and more hemispherical, though breeds used for cheese production incline towards the caprine form. The teats are cylindrical in young animals of both species, but in older animals — especially in goats of high productivity — they become conical and blend more smoothly into the contours of the gland. And the covering differs: the udder skin is finely haired in goats, while in sheep the upper part may be covered by the fleece.

That is the whole of the normal gland, from the line on the embryo to the fleece on the ewe's udder. If you want it in the cow specifically, and in place with the rest of the abdomen around it, our bovine anatomy guide is the next page; if you want the same comparative method applied to other organs, comparative veterinary anatomy is where it goes next.

14 Test yourself

One hundred and four questions across every section above. Cover the answers first — looking at an answer is not the same as retrieving it, and only one of the two is revision.

1 **Which four subjects does this page deliberately leave out?**

> ANSWER Four subjects are left out: **mastitis as a clinical subject**, mammary tumours and their management, milking machinery and dairy production management, and lactation endocrinology in its own right. The anatomy that bears on each is here; the clinical material is not.

2 **Which two textbooks carry this article, and what happens where they disagree?**

> ANSWER *Dyce, Sack and Wensing's Textbook of Veterinary Anatomy*, 5th ed., and *Bovine Anatomy: An Illustrated Text*, 2nd extended ed. Where they differ — as they do on the number of mammary lymph nodes — both are named and neither is dropped.

3 **What kind of gland is the mammary gland?**

> ANSWER A greatly modified, much enlarged **apocrine sweat gland**. Dyce places it in the chapter on the common integument, and the histologists classify it specifically as a modified apocrine sweat gland with a specialised secretory function.

4 **What is the mammary ridge?**

> ANSWER A **linear ectodermal thickening** that appears on each side of the ventral body wall in the embryo, between the primordia of the fore and hind limbs, and from which the mammary buds grow down into the mesenchyme. It is also called the milk line.

5 **Why do the adult glands end up on the belly rather than on the flank?**

> ANSWER Because the ridge is shifted ventrally as the dorsal part of the body wall grows faster than the ventral part.

6 **In which species does the ridge persist along essentially its whole length?**

ANSWER Carnivores and the pig — which is why their glands run from the thorax to the groin.

7 **In which species does only the inguinal part persist, and what is the consequence?**

ANSWER **Ruminants and horses.** The consequence is the udder: glands consolidated in the groin into a single mass.

8 **What decides how many mammary glands a species has?**

ANSWER How many mammary buds survive on the ridge. More buds appear than survive; most of the extra ones regress, and those that persist become supernumerary teats.

9 **What is a proliferation teat, and which species have one?**

ANSWER A teat formed by growth of the **areolar tissue** — the mesenchyme around the epithelial sprout — with the ring of skin around the bud completely taken up into the teat. Ruminants and the horse.

10 **What is colostrum for?**

ANSWER Passive immunity: it carries a high concentration of immunoglobulins to the newborn. Budras adds a second function — it is laxative, and helps the newborn pass meconium. In the cow it is produced for about the first five days.

11 **What two parts make up one mammary gland?**

ANSWER A **body** (*corpus mammae*) — the glandular mass with its duct system and framework — and a **teat** (*papilla mammae*).

12 **What is an udder?**

ANSWER Not an organ type but a **position**: what you call the mammary glands of a species in which they are consolidated in the groin into a single mass. Dyce applies the word to ruminants and horses, and also, with a caveat, to the sow's more separated glands.

13 **How many glands are in a cow's udder, and what are they called?**

ANSWER Four, called **quarters** — two forequarters and two hindquarters. Each has its own duct system, its own sinus and its own teat.

14 **What separates the right and left halves of a bovine udder?**

ANSWER The median **intermammary groove** externally, and the paired medial laminae of the suspensory apparatus internally. It is a real plane: the halves can be separated by blunt dissection along it.

15 **Is there a septum between the fore and hind quarter of the same side?**

ANSWER No. Dyce says the boundary is rarely distinct and Budras states there is no septum at all — even though the two duct systems are entirely separate.

16 **How large is a lobule, and how many alveoli does it hold?**

ANSWER About 1.5 × 1.0 × 0.5 mm, holding roughly **200 alveoli**. Budras compares it to a bunch of grapes; Dyce gives a lobule of 1 mm or a little more with about 200 alveoli, so the two agree.

17 **How thick and how long is a bovine teat, in the rule of thumb Budras gives?**

ANSWER About as thick as your thumb and about as long as your index finger.

18 **Name the drainage sequence from the alveolus to the outside.**

ANSWER Alveolus → alveolar lactiferous duct → intralobular duct → interlobular duct → lactiferous ducts of successive orders → collecting duct → gland sinus → annular fold → teat sinus → teat canal (papillary duct) → orifice.

19 **How many wide lactiferous ducts finally enter the lactiferous sinus?**

ANSWER About ten — Dyce gives "only 10 or so" in one place and "about a dozen" in another. The number to carry is around ten, not hundreds.

20 **What are milk knots?**

ANSWER The more superficial dilations of the lactiferous ducts, which may be **3 cm or more in calibre** and can be palpated through the skin when distended with milk.

21 **What holds milk in those dilations between milkings?**

ANSWER Contraction of the muscular wall of the **narrow portions** between them. The ducts alternate wider and narrower sections, which Dyce calls unusual.

22 **What is the capacity of the bovine lactiferous sinus?**

ANSWER Several hundred millilitres, taking the gland sinus and teat sinus together.

23 **What divides the gland sinus from the teat sinus?**

ANSWER The **annular fold** — a mucosal fold built on a submucosal ring of veins, the **venous circle of Fürstenberg**.

24 **A dairy clinician says "gland cistern" and "teat cistern". What are those in textbook terms?**

ANSWER The same two structures under their other name. **Cistern** is the plain-English gloss of *sinus lactifer*: the **gland cistern** is the gland sinus, the **teat cistern** is the teat sinus, and the **milk cistern** is the two together. Nothing anatomical changes with the word — the textbooks prefer *sinus* and the parlour prefers *cistern*.

25 **What can a particularly prominent annular fold do?**

ANSWER Impede milk flow. Dyce records that its prominence varies and that occasionally it is pronounced enough to do so.

26 **Why is the bovine mammary gland called a storage gland?**

ANSWER Because many alveoli connect directly with one another and the arrangement holds a large volume of milk between milkings, rather than delivering it continuously.

27 **What experiment shows that the quarters have separate duct systems?**

ANSWER Injecting different coloured dyes into different quarters: each stays in its own quarter. The latex-injected sagittal section in this article — green cranial, blue caudal — is the same demonstration photographed.

28 **A cow's quarter is an island in one sense and continuous with its neighbour in another. Explain both.**

ANSWER Down the **lumen** it is an island: each gland has one duct system and no communication with any other. Through the **tissue** it is not: the two quarters of one side have no septum between them. The right and left halves, by contrast, are genuinely partitioned by the medial laminae.

29 **"Apocrine" is used twice on this page for two different things. What are they?**

ANSWER As a **classification**, the mammary gland is a modified apocrine sweat gland — the kind of skin gland it descends from. As a **mechanism**, the apocrine mode of secretion is how milk fat is released. The gland is apocrine by ancestry and uses both apocrine and merocrine mechanisms in service.

30 **How does milk fat leave the lactocyte?**

ANSWER By the **apocrine mode**: the droplet is released wrapped in a piece of the apical cell membrane, so the fat globule in milk sits inside a membrane that used to be the cell's.

31 **How does milk protein leave the lactocyte?**

ANSWER By the **merocrine** mode — exocytosis. The proteins are made on the rough endoplasmic reticulum, processed by the Golgi apparatus, packaged into vesicles and released into the alveolar lumen. The cell loses nothing of itself.

32 **Where is lactose made, and how does it leave?**

ANSWER It is a product of the **Golgi apparatus** and leaves in the same vesicles as the milk protein, by exocytosis.

33 **Where does the immunoglobulin A in milk come from?**

ANSWER Not from the lactocyte. It is produced by **plasma cells**, either locally in the gland or arriving from the blood, and is transferred across the epithelium. It is particularly abundant in colostrum.

34 **What is a myoepithelial cell, and where does it lie?**

ANSWER An **ectodermal derivative** modified to carry contractile filaments, so that it behaves like a smooth muscle cell. It lies between the secretory cells and the basal lamina, wrapped around each alveolus and continuing as a looser network around the smaller ducts.

35 **What receptor does the myoepithelial cell carry, and what happens when it is activated?**

ANSWER An **oxytocin** receptor. Activation contracts the cell, narrows the alveolar lumen and forces milk into the duct system — let-down, or the milk ejection reflex.

36 **Trace the milk-ejection reflex from the teat and back.**

ANSWER Suckling or massage stimulates the **sensory nerves of the teat and udder skin**; the afferent stimulus reaches the hypothalamic nuclei, where oxytocin is produced; oxytocin is released through the neurohypophysis into the blood; the blood carries it to the gland, where it contracts the myoepithelial cells and presses milk into the ducts and sinus.

37 **What suppresses let-down, and how?**

ANSWER **Adrenaline**, secreted under stress, suppresses the action of oxytocin on the myoepithelial cells. The milk is still there; the mechanism that moves it has been switched off.

38 **Are all the lobules of one gland at the same stage of the secretory cycle?**

ANSWER No. Dyce records that active and non-active lobules may be present concurrently in the same gland, and that the height of the alveolar epithelium changes markedly through the cycle.

39 **How long is a bovine teat, and how thick is its wall?**

ANSWER Most often cylindrical and about **8 cm** long. The wall is generally about **6 mm** thick and increases to about **1 cm** at the lower end, where the papillary duct and its closing mechanism are.

40 **Name the three layers of the teat wall and what each is for.**

ANSWER An **outer** layer of dry, hairless, tightly bound skin without skin glands; an **intermediate** layer of smooth muscle and a dense venous plexus, forming a kind of erectile tissue; and an **inner** mucosa thrown into folds, yellowish generally and white in the papillary duct.

41 **Why do teat injuries bleed persistently?**

ANSWER Because the venous plexus of the intermediate layer forms an **erectile tissue**. Budras states directly that it makes haemostasis difficult in injuries or surgery of the teat.

42 **Name the three mechanisms that close the teat canal.**

ANSWER A **sphincter** of smooth muscle reinforced by elastic tissue; a **plug** of fatty desquamated cells produced by the stratified squamous lining between milkings; and the **longitudinal mucosal folds** that let the canal close on itself.

43 **What is Fürstenberg's rosette, and what hedge does Dyce attach to it?**

ANSWER The radial structure formed by the proximal ends of the longitudinal folds, at the boundary between the teat sinus and the teat canal. Dyce describes the same ridges and then adds that the arrangement is **rarely as distinct as traditionally described**.

44 **Name the four forms of the bovine teat extremity.**

ANSWER Funnel shaped, dish shaped, rounded and pointed. All four are normal.

45 **How does the mare's teat differ from the cow's?**

ANSWER It is small and cylindrical — larger and more conical in the lactating mare — and its apex is perforated by **two, occasionally three, openings**, each leading through its own short papillary duct to its own small lactiferous sinus.

46 **How do a goat's teats change with age?**

ANSWER They are cylindrical in young animals but tend to become conical in older does, especially high-yielding ones, and to blend more smoothly into the contours of the gland.

47 **How many mammary glands has the cow, the mare, the ewe, the sow, the bitch and the queen?**

ANSWER Cow **4**; mare **2**; ewe and doe **2**; sow **14** (seven pairs); bitch **10** (five pairs); queen **8** (four pairs).

48 **Where are the bitch's five pairs?**

ANSWER The two cranial pairs are **thoracic**, the next two **abdominal**, and the caudalmost pair **inguinal**.

49 **What hedges does Dyce put on the gland counts, and why do they matter?**

ANSWER Dogs **generally** have five pairs; the sow **almost invariably** has seven. These are typical numbers, not fixed ones — an animal with an extra pair is not abnormal.

50 **Where are the sow's glands, and how are they arranged?**

ANSWER In a double row extending from the thorax to the groin — almost invariably seven pairs. Each is pendulous and, though confluent with its neighbours at the base, otherwise clearly defined.

51 **Why does it matter that some of a sow's teats project to the side?**

ANSWER Because sows generally suckle while lying on their side, so those teats may not be readily accessible to the litter; the glands behind them may be little used and regress early.

52 **In the comparative figure, which column is not a domestic species, and why is it there?**

ANSWER The **woman**, with one pair of thoracic glands. She is in the source plate, and she is the reason a general search for mammary gland anatomy returns human anatomy — nipple in the fourth intercostal space, ligaments of Cooper, and so on, none of which belongs to any animal on this page.

53 **Describe the mare's udder.**

ANSWER Two glands consolidated in a rather small udder below the caudal abdominal floor and cranial part of the pelvis, concealed from casual inspection by the thigh, with a prominent external groove showing its formation from right and left halves. It is very small in young virgin animals.

54 **How do the goat's and the ewe's udders differ?**

ANSWER In the goat the two glands are more distinctly demarcated externally, and in milk goats the udder is large for the body size, deep and conical. In the ewe it is smaller and more hemispherical, though cheese breeds incline towards the caprine form.

55 **What single developmental fact fixes the number of orifices on a teat?**

ANSWER The number of **epidermal sprouts** that grow from the mammary bud. One sprout gives one duct system, one lactiferous sinus, one papillary duct and one orifice; more sprouts give correspondingly more of each.

56 **How many openings are there on a teat in the cow, mare, sow, bitch and cat?**

ANSWER Cow (and ewe and doe) **1**; mare **2**, occasionally 3; sow **2**; bitch **10 or 12**; cat **4 to 8**.

57 **In the mare, what lies behind each of the two teat openings?**

ANSWER Its own short papillary duct leading to **its own small lactiferous sinus**, spread between the teat and the gland mass, with its own independent set of lactiferous ducts.

58 **Can the independence of the mare's two gland units be shown by dissection?**

ANSWER No. Dyce records that the tissues of the individual glands of each side interdigitate, and that it is impossible to demonstrate their independence on dissection.

59 **What does Budras contrast the cow with, on duct systems?**

ANSWER With the bitch and the mare: in contrast to those, each mammary gland of the cow contains only **one** duct system and its associated glandular tissue.

60 **What is the difference between hyperthelia and hypermastia?**

ANSWER **Hyperthelia** is supernumerary teats — from the Greek *thele*, nipple. **Hypermastia** is supernumerary glands.

61 **Where do supernumerary teats usually sit in the cow, and how common are they?**

ANSWER Usually caudal to the normal teats, but they may lie between them or cranial to them. Dyce calls accessory teats in the cow very common, and not uncommon in goats.

62 **What is the only consequence of a supernumerary teat that this page states?**

ANSWER A mechanical one: a teat sitting on a main teat interferes with milking, which is why such teats are often removed from the udders of cows and goats. They may also be associated with functional glandular tissue — an accessory teat is not necessarily blind.

63 **Where do the medial laminae arise, and what are they made of?**

ANSWER Mainly from the **tunica flava** — the yellow abdominal tunic — on the outer surface of the prepubic tendon at its junction with the symphyseal tendon, and in small part from the symphyseal tendon itself. They are largely **elastic** tissue.

64 **Where do the lateral laminae arise, and what are they made of?**

ANSWER From the lateral crus of the superficial inguinal ring and, behind that, from the medial femoral fascia and the symphyseal tendon. They are **dense regular collagenous** tissue.

65 **What are the suspensory lamellae, and where do they come from?**

ANSWER Thin sheets detached from both laminae as they run ventrally. They penetrate the gland and divide the parenchyma into curved, overlapping lobes, carrying the vessels and nerves with them — which is also why both laminae thin as they are followed downwards.

66 **Why does the medial part of a heavily laden udder sag, and why do the teats point outwards?**

ANSWER Because the medial laminae are elastic and the lateral laminae are not. Under load the elastic sheet stretches more than the fibrous one, the floor of the udder drops between them, and the teats are carried laterally and cranially.

67 **What does Dyce record as the occasional endpoint of the load on the suspensory apparatus?**

ANSWER That ever-increasing demands for milk production place a heavy and sometimes unsustainable burden on it, **which occasionally ruptures** — a disastrous outcome.

68 **Why is it anatomically possible to remove one lateral half of an udder?**

ANSWER Because the medial laminae are **paired and paramedian** rather than single, so there is a genuine cleavage plane between the two halves. Budras notes the separation can be shown by blunt dissection between them from their caudal borders.

69 **How does the mare's suspensory apparatus compare?**

ANSWER The same design, much less developed: medial elastic and lateral fibrous ligaments which together encapsulate the udder and supply the lamellae that support the parenchyma.

70 **How much blood does a litre of milk cost?**

ANSWER Budras gives up to **600 litres** of blood flowing through the udder per litre of milk. It is an estimate, and the point is the order of magnitude: it is why the vessels of the udder are out of all proportion to its size.

71 **What is the main artery of the bovine udder, how big is it, and how does it get there?**

ANSWER The **external pudendal artery**, with a diameter that may exceed **15 mm**, passing through the **inguinal canal** accompanied by a satellite vein, lymphatics and nerves.

72 **What does the external pudendal artery divide into at the base of the udder?**

ANSWER Two divergent branches, the **cranial** and **caudal mammary arteries**, one running forward and one back, both partly or wholly embedded in the gland substance.

73 **What contribution does the ventral perineal artery make?**

ANSWER Its division anastomoses with the caudal mammary artery, but the contribution is restricted to the mammary lymph nodes and a limited portion of the hindquarter.

74 **What is the venous ring, and what forms it?**

ANSWER A ring of veins above the base of the udder, formed by paired veins connected across the midline by transverse vessels — the right and left cranial mammary veins anastomosing in front and the caudal mammary veins behind. Many of the udder's veins simply join it.

75 **By what two routes does blood leave the bovine udder?**

ANSWER By the **external pudendal veins**, passing back through the inguinal canals, and by the **subcutaneous abdominal (milk) veins**, running forward over the abdominal floor and entering the body wall at the **milk well** to reach the internal thoracic veins.

76 **The same veins have two names each. Give the pairs.**

ANSWER The **cranial mammary vein** is the caudal superficial epigastric vein. The **subcutaneous abdominal vein** — the visible milk vein — is the cranial superficial epigastric vein.

77 **How does a milk vein come into existence?**

ANSWER In the calf and heifer, the cranial and caudal superficial epigastric veins drain separate territories in **opposite directions**, each with valves enforcing its direction. During the first pregnancy the increased flow through the enlarging udder distends the veins, the valves become incompetent, and the two territories unite into one continuous channel in which blood can flow either way.

78 **What is the functional advantage of that united channel?**

ANSWER It assures effective venous drainage if some channels are occluded — for instance in the recumbent cow lying on one side.

79 **Is the milk vein a good site for intravenous injection or blood sampling?**

ANSWER It is sometimes used, but Dyce's verdict is that **it is not a wise choice**: its varicosed structure predisposes it to troublesome leakage.

80 **How is the sow's mammary blood supply different, and why must it be?**

ANSWER It comes from local vessels — the internal thoracic and the cranial and caudal superficial epigastric arteries — rather than from one dominant trunk. A row of fourteen glands from chest to groin cannot be fed through one inguinal canal.

81 **Does the mare develop a milk vein?**

ANSWER Yes. Dyce records that, as in the cow, a subcutaneous venous connection with a superficial vein of the thoracic wall develops as an alternative drainage route during the first pregnancy.

82 **Where are the bovine mammary lymph nodes, and how are they palpated?**

ANSWER Above the caudal part of the udder, on the surface applied to the body wall and **deep to the lateral lamina** of the suspensory apparatus. Budras gives the landmark: between the thighs, about 6 cm from the skin, at the caudal attachment of the udder.

83 **How can the big lymphatics of the udder be told from the subcutaneous veins?**

ANSWER By direction. The large lymph vessels show through the skin and run **caudodorsally**; the subcutaneous veins run **craniodorsally**.

84 **Where does lymph from the mammary nodes go next, and can that node be reached?**

ANSWER To the **deep inguinal** node — the iliofemoral node — in the angle between the deep circumflex and external iliac arteries. Dyce records that it may be palpated per rectum.

85 **How many mammary lymph nodes are there? Answer carefully.**

ANSWER The books differ. Dyce says **generally two on each side**, one large and one much smaller; Budras says **one to three** superficial inguinal nodes, with small intramammary nodes possibly also present. Say one to three, usually two, and name the source.

86 **Why does the sow's mammary lymph drain in two directions?**

ANSWER Because her glands run from the chest to the groin. The first two — or three — pairs drain to the **ventral superficial cervical** nodes and the remainder to the superficial inguinal nodes.

87 **What does Dyce say about the lymph pathways of the bitch and the queen?**

ANSWER That they are **erratic**, and that some lymph may cross the midline. In the cat it is said that the vessels do not cross the midline nor penetrate the thoracic wall. The cranial glands drain to the axillary and sternal nodes, the caudal to the superficial inguinal.

88 **Which single nerve supplies the substance of the bovine gland and the deep teat wall?**

ANSWER The **genitofemoral nerve**, alone, reaching the udder through the inguinal canal.

89 **Which nerves supply the skin and teats of the fore and hind quarters?**

ANSWER Forequarters and the cranial part of the base: the iliohypogastric nerve, the ilioinguinal nerve and the **cranial branch** of the genitofemoral. Hindquarters: the **caudal branch** of the genitofemoral and the mammary branch of the pudendal nerve.

90 **Why is the sensory supply of the udder skin more than sensation?**

ANSWER It is the **afferent pathway of the neurohormonal reflex arc** that initiates and maintains milk expulsion. Cut the sensation and the reflex that empties the gland is cut with it.

91 **What is a newborn calf's udder mostly made of?**

ANSWER **Fat.** At full term the gland has short but well-formed teats, small sinuses and the first branches of the duct systems, and the bulk of the organ is fat.

92 **Describe the two different kinds of growth between birth and first conception.**

ANSWER First, growth that **keeps pace with the body** and is entirely deposition of fat. Then, commencing **well before puberty**, growth that outruns the body, in which the duct system and gland tissue develop rapidly — attributed to cyclical oestrogen, on the evidence that spurts occur directly before ovulation. The gland then rests until the first pregnancy.

93 **What grows in the first half of the first pregnancy, and what in the second?**

ANSWER Ducts in the first half; **secretory tissue** in the second, displacing the space-occupying fat as it grows.

94 **What is lactogenesis, and what triggers it?**

> ANSWER The start of milk secretion by the lactocytes. Towards the end of gestation a lumen develops in the still partly solid glandular end-pieces under progesterone and oestrogen, and under **prolactin** the lactocytes begin to secrete.

95 **Which quarters stay in production after calving?**

> ANSWER Only those that are emptied. Budras states that secretion is maintained only in the quarters the suckling uses, and the unused quarters rapidly undergo involution.

96 **Why does more frequent milking increase yield?**

> ANSWER Because the act of milking itself stimulates the release of prolactin, oxytocin and corticotropin — so more frequent milking, within limits, increases the yield.

97 **What happens to the gland tissue at involution, and does the udder return to its old size?**

> ANSWER The secretory cells of the alveoli and alveolar lactiferous ducts degenerate and the glandular tissue is **replaced by fat and connective tissue**. The udder gets smaller but **never returns** to its pre-lactation size, and grows a little more with each pregnancy.

98 **How long is a dairy cow's dry period, and what is it for?**

> ANSWER About **60 days** before calving, after a lactation of about ten months, produced by decreasing the ration and reducing milking.

99 **Do males have mammary glands?**

> ANSWER Yes — the ridge forms in both sexes, buds form in male embryos, and they persist as rudimentary teats. Normally the male gland remains at the calf stage throughout life.

100 **Where are the male rudimentary teats in the ruminant, the carnivore and the horse?**

> ANSWER In ruminants, on the **cranial surface of the scrotum**. In carnivores and the pig, on the ventral surface of the trunk. In horses they are less common, and occasionally appear beside the prepuce.

101 **Can a male's mammary gland be made to grow?**

> ANSWER Yes. Budras records that during puberty some bull calves undergo a further temporary growth of the mammary glands under an elevated level of oestrogen, exactly as is natural in the female. The tissue is not different; the hormonal environment is.

102 **Is "males keep rudimentary teats" true of all mammals?**

> ANSWER No. Dyce records that in certain species such as rats the male glands regress completely.

103 **Name four kinds of variation on this page that are normal and could be mistaken for a lesion.**

> ANSWER The four forms of the teat extremity; the varying prominence of the annular fold; Fürstenberg's rosette, which is rarely as distinct as the textbooks draw it; and the number of mammary lymph nodes, which is one to three.

104 **How does the covering of the udder differ between the goat and the ewe?**

> ANSWER The udder skin is finely haired in goats; in sheep the upper part may be covered by the fleece.

15 Mammary Gland Anatomy — frequently asked questions

How many mammary glands does a cow have, and how many does a dog have?

A cow has **four**, consolidated into one udder and called quarters — two forequarters and two hindquarters, each with its own duct system, its own lactiferous sinus and its own teat. A dog generally has **five pairs**, that is ten glands, spread along the ventral trunk: two thoracic pairs, two abdominal and one inguinal. The difference is embryological rather than functional. The mammary ridge, a line of ectoderm running from the axilla to the groin, persists along essentially its whole length in carnivores and the pig, but only in the inguinal region in ruminants and horses — and the glands can only form where the ridge survived.

Why does a cow's teat have one hole and a dog's have ten?

Because of how many epidermal **sprouts** grew from the mammary bud before birth. One sprout produces one duct system, which produces one lactiferous sinus, one papillary duct and one orifice; more sprouts produce correspondingly more of each, each with its own glandular mass and its own independent opening. The cow, the ewe and the doe take the one-sprout route, so a single very large duct system fills the whole gland. The mare and the sow have two sprouts and two openings per teat. The bitch's teat is perforated by **10 or 12** fine openings and the cat's by **4 to 8**, each the outlet of a separate small sinus. The number is settled before birth and does not change.

What holds a cow's udder up?

The **suspensory apparatus**: two sheets of fascia with different mechanical properties. The **medial laminae** are largely elastic and arise mainly from the tunica flava — the yellow abdominal tunic — on the prepubic tendon; being paired and paramedian, they also form the plane between the two halves of the udder. The **lateral laminae** are dense collagenous tissue arising from the lateral crus of the superficial inguinal ring and the medial femoral fascia, and they pass over the outer surface of each half. From both, thin **lamellae** run into the gland and divide the parenchyma into overlapping lobes. Because the medial sheet stretches and the lateral one does not, a full udder sags in the middle and its teats point outwards and forwards.

What is the milk vein, and why is it so large in a dairy cow?

It is the **subcutaneous abdominal vein** — also called the cranial superficial epigastric vein — running forward under the skin of the abdominal floor and entering the body wall through a palpable opening called the **milk well**, to join the internal thoracic vein. It is large because it is not one vein but two that merged. In the calf and the heifer, the cranial and caudal superficial epigastric veins drain separate territories in opposite directions, each with valves enforcing its direction. During the first pregnancy the greatly increased blood flow through the enlarging udder distends them, the valves become incompetent, and the two territories unite into one continuous channel through which blood can flow either way. Dyce notes it is sometimes used for injection or sampling, and that this is **not a wise choice**: its varicosed structure leaks.

What is the difference between the gland sinus and the teat sinus?

They are the two parts of one cavity, the **lactiferous sinus**, which in the cow holds several hundred millilitres. The **gland sinus** is the upper part, inside the body of the gland, and the collecting ducts of the lobes open into it. The **teat sinus** is the lower part, inside the teat, and it is what the teat canal drains. Between them lies the **annular fold** — a fold of mucosa built on a submucosal ring of veins known as the venous circle of Fürstenberg. Its prominence varies between animals, and Dyce records that occasionally it is pronounced enough to impede the flow of milk.

Is a cow's mammary gland really a sweat gland?

Yes, and it is classified as one rather than merely compared to one. Dyce places the mammae in the chapter on the common integument, immediately after the sweat glands, and describes them as **greatly modified, much enlarged sweat glands** whose secretion nourishes the young; the histologists are more specific and classify the gland as a modified **apocrine** sweat gland. That classification is not a curiosity. It is why the gland, its ducts and its contractile myoepithelial cells are all ectodermal derivatives, why its architecture is a skin gland's architecture scaled up into a compound tubuloalveolar gland, and why its position on the body was decided by a line of ectoderm in the embryo rather than by the organ it feeds.

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