ANATOMY AND HISTOLOGY OF THE GUT OF THE EMU
DROMAIUS NOVAEHOLLANDIAE

The Emu *Dromaius novaehollandiae*, a large ratite, has a distribution which includes the arid interior of Australia. The diet of the Emu consists largely of herbage, with shoots, seeds, fruits, insects and flowers being eaten when seasonally abundant (Davies 1978; Dawson *et al.* 1984). Emus can satisfy a large portion of their daily energy needs from the digestion of plant fibre (Herd & Dawson 1984). As no vertebrate is able to synthesize the enzymes necessary to digest plant fibre, many herbivores, including a number of birds, use a symbiotic relationship with microorganisms in their gut to digest cell walls. The extent of the degradation of plant fibre depends upon the composition of the gut microflora, its retention time in the fermentative parts of the gut and the nature of the plant cell wall (Uden 1978). Thus the guts of most herbivorous species provide capacious regions for retention and degradation of plant material.

Elongation of the hindgut, particularly enlargement of the caeca, is observed in many avian herbivores (Leopold 1953; Fenna & Boag 1974a). The gut of the domestic chicken has been described by Hodges (1974), but little is published on the histology of the gut of other herbivorous birds, including the Emu. Knowledge of the anatomy of the gut of the Emu is essential to understanding how it digests the plant material in its diet. I present here a histological description of the gut of the Emu.

I used two adult Emus (bodyweights 32 and 53 kg) which had been reared in captivity and held in a 1 ha yard of dry sclerophyll forest. They were maintained on a diet of natural forage supplemented with commercially prepared stock cubes (15% crude protein; 33% neutral detergent fibre; 12 kJ per gram metabolizable energy). The Emus were killed with an overdose of suxamethonium chloride and their digestive tracts quickly excised and measured. Tissues for histological examination were fixed in buffered formalin, mounted in paraffin wax, and sections (7 to 10μm) were stained with haematoxylin and eosin (McManus & Mowray 1960). In addition, the proventriculus and gizzard were examined for the presence of oxyntico-peptic cells following the procedure of Menzies & Fisk (1963). A domestic duck *Anas platyrhynchos* was killed and its gut measured and compared with that of the Emu.

STRUCTURE OF THE GUT

The oesophagi were 0.70 and 0.79 m long, or about 17% of the total gut length (Table I), and their structure relatively uniform. They were lined with a stratified squamous epithelium underlaid by loose connective tissue, the tunica propria (Plate 1A). The secretions of numerous mucous glands embedded in the tunica propria may serve to lubricate food as it is propelled down the oesophagus. Outside the tunica propria was a band of longitudinal muscle, the muscularis mucosae, separated from the muscularis externa by a thin layer of connective tissue, the submucosa. The muscularis externa consists of a broad inner band of circular muscle and a thin outer layer of longitudinal muscle. There is no crop, but the mucous membrane is arranged in longitudinal folds which allow distension when bulky food items are swallowed. Captive Emus fed chopped apple retained portions of fruit in their distal oesophagus for 30 minutes, suggesting that stretching of the oesophagus may facilitate the storage of some food in the absence of a crop.

The proventriculus or glandular stomach is a thick-walled organ lying between the oesophagus and gizzard. The proventriculus and gizzard together form about 5% of the total gut length. The proventriculus has a large lumen suggesting that it could also store food in the absence of a crop. Across the mucosal surface are raised papillae through which pass the primary ducts of the proventricular glands. These glands are the major component of the thick, spongy walls of the proventriculus and open distally (Plate 1B). The gland consists of a primary duct into which drain the secretions of the glandular alveoli (Plate 1C). Staining showed that oxyntico-peptic cells lined the glandular alveoli (Plate 1D). Thus gastric digestion of food may commence when it is moistened with these secretions in the proventriculus. The proventricular gland of the Emu is simpler than that in chickens, which consists of several small groups of lobules each composed of numerous alveoli (Hodges 1974).

Gastric proteolysis continues in the gizzard or ventriculus, assisted by a highly acid environment and grinding with small stones and grit. The pH of the proventriculus and gizzard is 2.8 and 2.5 respectively (Davies 1978), values similar to those in poultry (Hill 1971). The gizzard has a thick muscular wall and an abrasion-resistant lining of a keratin-like protein (Hodges 1974). The gizzards examined contained gastroliths, pebbles up to 30 mm in length whose edges were worn by grinding. These pebbles are probably deliberately ingested to assist in the mechanical breakdown of food. Below the

TABLE I

The Dimensions of the Gut of some Avian Herbivores.

Species	Body Weight (BW) (kg)	Oesophagus length (m)	Oesophagus % total length	Proventriculus plus Gizzard length (m)	Proventriculus plus Gizzard % total length	Small Intestine length (m)	Small Intestine % total length	Small Intestine length/BW (m.kg⁻¹)	Caecum length (m)	Caecum length/BW (m.kg⁻¹)	Rectum length (m)	Rectum % total length	Rectum length/BW (m.kg⁻¹)	Total gut+ length (m)	Total gut+ length/BW (m.kg⁻¹)	Reference
Red grouse[1]																
Wild	0.65	—	—	—	—	0.99	—	1.52	1.44	2.22	—	—	—	—	—	Moss (1972)
Captive	0.65	—	—	—	—	0.72	—	1.11	0.78	1.20	—	—	—	—	—	Moss (1972)
Willow ptarmigan	0.53	—	—	—	—	0.91	—	1.73	0.47	0.90	0.13	—	0.24	—	—	Leopold (1953)
Chicken	2	0.31	13	0.06	3	1.88	78	0.94	—	—	0.15	6	0.08	2.40	1.20	Feltwell & Fox (1978)
Japanese quail	0.11	—	—	—	—	0.39	—	3.56	0.06	0.50	—	—	—	—	—	Fenna & Boag (1974a)
Ringed-necked[2]																
Pheasant	1.27	—	—	—	—	1.01	—	0.80	0.20	0.16	0.11	—	0.09	—	—	Leopold (1953)
Domestic duck	2.2	0.31	12	0.13	5	2.11	80	0.96	0.14	0.06	0.09	3	0.04	2.64	1.20	This study
Emu	32	0.70	22	0.20	6	1.97	63	0.06	0.14	0.004	0.25	8	0.01	3.12	0.10	This study
	53	0.79	12	0.26	4	5.20	79	0.10	0.12	0.002	0.30	5	0.01	6.55	0.12	

+ Excludes caeca. Gaps in the table represent data not available from the references.

[1] *Lagopus lagopus stoticus*   [2] *Phasianus colchicus*

abrasion-resistant lining is a glandular mucous membrane, a thin tunica propria and submucous, and then extensive layers of circular muscle. Gizzard glands extend down to the submucosa through pits in the inner lining of the gizzard (Plate 2A). These glands are lined by chief cells which degenerate along the pit of the gland to become surface epithelium cells. The production of the proteolytic enzyme pepsin is suggested by the presence of Bowie-positive granules in the chief cells.

The lengths of the small intestine, paired caeca, and rectum are much shorter than those of other avian herbivores when compared on a bodyweight basis (Table I). The histological structure of the three organs is similar (Plates 2B, C, D). The increased surface area of the mucous membrane provided by folds and villi would be expected to enhance the absorption of nutrients through an epithelium dominated by columnar cells. Goblet cells appear to secrete mucus which would assist the passage of digesta, these cells being most common along the distal rectum. A few enterochromaffin cells are present along the duodenum, and in chickens these cells contain the hormone 5-hydroxytryptamine (Hodges 1974).

Between villi numerous crypts of Lieberkuhn are present in the tunica propria, the latter also forms the core of the villi. Villi along the proximal caecum are well developed and the crypts of Lieberkuhn very shallow. Villi remain well developed along the length of the caeca becoming less numerous in the distal region where they are separated by small gaps, and few crypts are present (Plate 2C). The arrangement of villi in the proximal caecum is similar to that reported in Japanese Quail *Coturnix coturnix* and Spruce Grouse *Canachites canadensis*. In the latter species the villi provide a separating mechanism to ensure only fluid and small particles of plant material enter the caeca and are retained for microbial degradation (Fenna & Boag 1974a).

There is a slight reduction in wall thickness from the duodenum to the distal small intestine and along the caeca due to a reduction in the muscle layers of the muscularis externa. The muscularis mucosae and submucosa are generally present only as thin layers. These layers are thicker in the rectum and the villi are well developed giving the rectum a large absorptive surface (Plate 2D). The histological structure of the rectum of
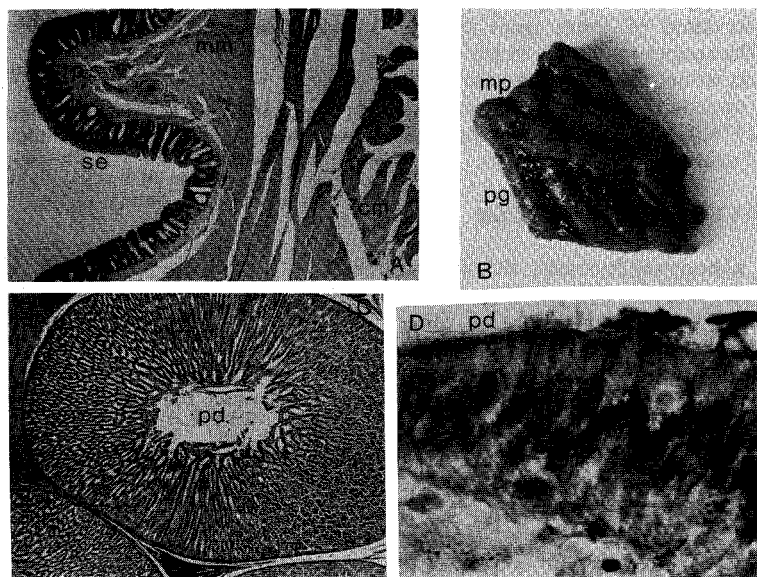
PLATE 1

Plate 1. A – T.S. proximal oesophagus, x50; B – Piece of proventricular wall showing mucosal papillae (mp) on the mucosal (upper) surface and proventricular glands (pg) below in the section cut through the wall, x3; C – T.S. proventricular gland, x35; D – L.S. proventricular gland showing Bowie-positive granules or pepsinogen amidst background of under-differentiated Altmann-positive granules, x1400. Abbreviations: cm – circular muscle of muscularis externa; L.S. – longitudinal section; mm – muscularis mucosae; pd – primary duct; se – squamous epithelium; tp – tunica propria; T.S. – transverse section.
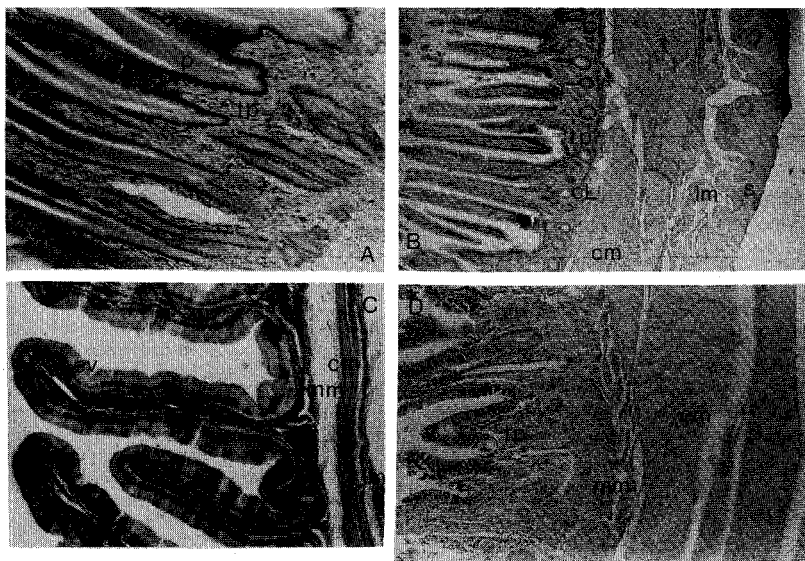
PLATE 2

Plate 2. A – L.S. gizzard glands, x180; B – T.S. distal small intestine, x50; C – T.S. distal caecum, x60; D – T.S. rectum, x90. Abbreviations: cL – crypt of Lieberkuhn; cv – corium of villus; ev – epithelium of villus; lm – longitudinal muscle of muscularis externa; p – pit; s – serosa; others as in Plate 1.

the Emu has been previously described by Johnson & Skadhauge (1975) who suggest that its large surface area may aid in the conservation of water from ureteral urine. In other birds the rectum may serve in storage of digesta prior to its excretion, assist in the retrograde movement of urine towards the caeca (Akester *et al.* 1967; Fenna & Boag 1974b), and participate in the post-renal modification of urine (Skadhauge 1973).

IMPLICATIONS FOR FIBRE DIGESTION

When compared on a bodyweight basis, the various segments of the Emu's hindgut, and particularly the paired caeca, are much shorter than those of other herbivorous birds (Table I), suggesting that the Emu has a relatively smaller capacity in which to retain plant material for fermentation. This contrasts to the situation in mammalian herbivores where the relative capacity of the gut increases as body size increases (Parra 1978). Associated with the simple structure of the gut, the rate of passage of feed residues through the Emu is rapid and should not facilitate fermentative digestion (Herd & Dawson 1984). However, Emus consuming four diets with neutral detergent fibre contents from 26 to 36% digested between 35 and 45% of the fibre, yielding energy equivalent to 12 to 63% of their standard metabolic rate and capable of satisfying 10 to 50% of their daily maintenance requirements for energy (Herd & Dawson 1984). Part of the explanation for the significant level of digestion of fibre by Emus may lie in the way avian herbivores subject fibre to gastric grinding and digestion, prior to fermentation. Hemicellulose in particular may be hydrolysed by gastric pepsin at low pH (Parra 1978).

The Emu has a lower standard metabolic rate than many other birds (Calder & Dawson 1978) and may not need the same relative expansion of the hindgut, augmented by large caeca, observed in smaller avian herbivores to obtain a similar energetic benefit from fermentation. For example, Willow Ptarmigan *Lagopus lagopus* (average weight 550 g; standard metabolic rate of 315 kJ per day) had 7 g of digesta (1.2% of bodyweight) fermenting in their caeca which produced 24 kJ of metabolizable energy, or 11% of their daily requirement (Gasaway 1976). Two Emus (average weight 35 kg), consuming low quality herbage during drought, had virtually nothing in their caeca (contents were only 5 g or 0.01% of bodyweight). However, they had 1.4 kg of digesta (4% of bodyweight) fermenting in their ileum and rectum which contributed the equivalent of 429 kJ of metabolizable energy per day or 13% of their standard metabolic rate (3,283 kJ per day), and this level of contribution was probably a considerable underestimate of the actual level (Herd & Dawson 1984). The Emu, by virtue of its large body size and low metabolic rate, may

be capable of gaining a significant portion of its daily energy requirement from the digestion of plant fibre, despite having a relatively simple hindgut.

REFERENCES

AKESTER, A.R., R.S. ANDERSON, K.J. HILL & G.W. OSBALDISTON. 1967. A radiographic study of urine flow in the domestic fowl. Br. Poult. Sci. 8: 209-215.

CALDER, W.A. & T.J. DAWSON. 1978. Resting metabolic rates of ratite birds: the kiwis and the emu. Comp. Biochem. Physiol. 60A: 479-481.

DAVIES, S.J.J.F. 1978. The food of emus. Aust. J. Ecol. 3: 411-422.

DAWSON, T.J., D. READ, E.M. RUSSELL & R.M. HERD. 1984. Seasonal variation in daily activity patterns, water relations and diet of emus. Emu 84: 93-102.

FELTWELL, R. & S. FOX. 1978. Practical Poultry Feeding. London: Faber and Faber.

FENNA, L. & D.A. BOAG. 1974a. Adaptive significance of the caeca in Japanese quail and spruce grouse (Galliformes). Can J. Zool. 52: 1577-1584.

———. 1974b. Filling and emptying of the galliform caecum. Can. J. Zool. 52: 537-540.

GASAWAY, W.C. 1976. Volatile fatty acids and metabolizable energy derived from cecal fermentation in the willow ptarmigan. Comp. Biochem. Physiol. 53A: 115-121.

HERD, R.M. & T.J. DAWSON. 1984. Fibre digestion in the emu *Dromaius novaehollandiae*, a large bird with a simple gut and high rates of passage. Physiol. Zool. 57: 70-84.

HILL, K.J. 1971. The structure of the alimentary tract. *In* Physiology and Biochemistry of the Domestic Fowl. Vol. 1. Eds. D.J. Bell and B.M. Freeman. London: Academic Press.

HODGES, R.D. 1974. The Histology of the Fowl. London: Academic Press.

JOHNSON, O.W. & E. SKADHAUGE. 1975. Structural-functional correlations in the kidney and observations of colon and cloacal morphology in certain Australian birds. J. Anat. 120: 495-505.

LEOPOLD, A.S. 1953. Intestinal morphology of gallinaceous birds in relation to food habits. J. Wildl. Manage. 17: 197-203.

McMANUS, J.F.A. & R.W. MOWRAY. 1960. Staining Methods. New York: Paul B. Hoeber Inc.

MENZIES, G. & A. FISK. 1963. Observations on the oxyntico-peptic cells in the proventricular mucosa of *Gallus domesticus*. Q. J. Microsc. Sci. 104: 207-215.

MOSS, R. 1972. Effects of captivity on gut lengths in red grouse. J. Wildl. Manage. 36: 99-104.

PARRA, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. *In* The Ecology of Arboreal Folivores. Ed. G.G. Montgomery. Washington, D.C.: Smithsonian Institution Press.

SKADHAUGE, E. 1973. Renal and cloacal salt and water transport in the fowl (*Gallus domesticus*). Dan. Med. Bull. 20: 1-82.

UDEN. P. 1978. Comparative studies on rate of passage, particle size and rate of digestion in ruminants, equines, rabbits and man. Unpublished Ph.D. Thesis. Cornell Univ.

DR ROBERT M. HERD, *Agricultural Research Centre, New South Wales Department of Agriculture, Trangie, NSW 2823.*

10 November 1983