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The Irradiation of Meat

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The present almost world-wide interest in the possibilities of using ionizing radiation such as gamma and cathode rays for the preservation of foods has grown from the broad research programme initiated by the United States Quartermaster Corps over a decade ago. The irradiation of meat has been one of the main areas of investigation.

MEAT irradiation applications may be classified according to dose as sterilization (high dose) or pasteurization (moderate dose). The unit of radiation dose most commonly used is the rad, which corresponds to an energy absorption of 100 ergs per gram.

The basic problem with both treatments is to determine the dose necessary for microbiological control, and then to investigate the effect of this dose on the particular product. For convenience, sterilization and pasteurization treatments will be considered separately.

Sterilization Treatments

The dose-mortality curve for microorganisms approaches the 100% mortality axis asymptotically, so no dose guarantees absolute sterility. This situation is similar to that encountered in heat processing, and so far it has been assumed that the microbiological requirements for commercial sterility will be similar for both heat and radiation processing. The radiation resistance of microorganisms does not, however, parallel their heat resistance.

Microorganisms vary widely in their sensitivity to radiation. The radiation resistance of some common food spoilage organisms is given by Thatcher (1963), Erdman, Thatcher, and MacQueen (1961), and Niven (1958). The most resistant pathogenic organisms present will determine the minimum radiation dose necessary for the safe storage of foods. For non-acid foods such as meat, *Clostridium botulinum* spores appear to be the most resistant of the pathogens and the dose for sterilization then appears to be near 4·5 million rads, based on an inactivation factor of 10^{12}, according to Wheaton and Pratt (1962) and Schmidt, Nank, and Lechowich (1962). A non-sporing spoilage bacterium, *Micrococcus radiodurans*, has been found by Duggan, Anderson, and Elliker (1963) to have apparently higher radiation resistance, and other relatively radiation-resistant organisms are discussed by Dupuy (1963). The effect these organisms may have on the sterilizing dose required for foods has not been fully explored.

Environmental factors which affect the radiation resistance of microorganisms have been described by Davydoff-Alibert (1963). Resistance is usually much higher in complex growing media such as food than in simpler media. It is also increased when the oxygen tension is reduced, and it is affected by temperature. Kaplan, Smith, and Tomlin (1962) found that substances that sensitize microorganisms include oxygen, nitric oxide, and some halogenated pyrimidines; and Bridges (1962) studied sensitivity induced by n-ethylmalimide. The main group of protective compounds contain sulphur, for example cysteine and cysteamine. Thus the sterilization dose may vary with the application. Other factors such as type of radiation and dose rate may affect radiation resistance, according to Bonet-Maury (1963) and Ley (1963). However, the effect of these factors over the range of conditions expected in a commercial irradiation plant appears to be small.

Radiation doses considerably lower than those necessary to sterilize foods severely damage meats. Strong off-odours and off-flavours develop, texture is lost, and while the colour of red meats in some instances may be retained temporarily, brown and green colours develop ultimately. Lawrie *et al.* (1961) have investigated the effect of irradiation on the pH, water-binding capacity, and proteolysis of raw beef and pork during storage.

When prolonged storage is contemplated another serious disadvantage, investigated by Doty and Wachter (1955), is that enzyme systems are not inactivated. Chiambalero, Johnson, and Drake (1959) and Pearson, Bratzler, and Costilow (1960) have shown that the only practicable way of controlling enzyme activity so far is through a short heat treatment.

Means of reducing the overlap between the sterilization dose and the dose that damages the product have been sought. Unfortunately, while the radiation sensitivity of meats and microorganisms can be altered, most procedures affect both to approximately the same extent, so there is no net gain. Freezing was found by Ingram *et al.* (1959) to be an exception. They noted that at −78°C, *Clostridium botulinum* spores were not protected to the same extent as the vegetative organisms or the meat itself. As these spores determine the sterilization dose, an overall gain which could exceed a factor of 2 was obtained. Samples so treated were still considered to be of indifferent quality.

Recently (Anon. 1963) bacon irradiated at the U.S. Army's Radiation Laboratory, Natick, was found to be in excellent condition after two years' storage at 70°F. This indicates considerable progress in overcoming the problems involved in radiation sterilization.

Pasteurization Treatments

The difficulties encountered with sterilization treatments have resulted in much attention being paid to advantages of lower radiation doses. Applications attracting most interest at present are the treatment of fish, meat, and poultry to extend their storage life as chilled produce, and the elimination of salmonella food-poisoning organisms from meat.

The second application is being investigated by Ley (1962) in the United Kingdom as a means of controlling salmonella contamination in raw frozen horse meat imported for pet food. A dose of 0·65 million rads is considered adequate for this purpose; this dose did not affect the palatability of the meat in a few tests carried out with dogs.

Extension of chilled storage has been investigated for some years. Wolin, Evans, and Niven (1957) observed that the shelf life of fresh meat inoculated with moderate numbers of pseudomonads and held at −20°C may be extended 4 to 5 times by an irradiation dose of approximately 50,000 rads. Carver and Steinberg (1959) observed various extensions of the storage life of chilled irradiated fish. The delay in microbiological spoilage of the irradiated product is apparently due to the high radiation sensitivity of the psychrophilic pseudomonads, the principal microorganisms causing spoilage of fresh meats at low temperatures.

While pasteurization treatments may delay microbial spoilage, the effect on storage life may be limited by other deteriorative processes. Coleby (1959) found that although a dose of 800,000 rads extended the time for putrefactive spoilage of whole chickens stored at 1°C by a factor of 5, the birds suffered a continual loss in acceptability which was apparent after the storage life had been extended by a factor of approximately 1·5. Oxidative rancidity is also accelerated by irradiation, and Lea, Macfarlane, and Parr (1960) noted that it may be a problem when irradiated meats are stored in the presence of oxygen. Estimates of the extension of storage will obviously depend on the standard adopted for organoleptic acceptability.

The combination of antibiotics such as chlortetracycline with radiation and refrigeration can give a further extension of the storage life of irradiated meat and fish, as shown by the work of Niven and Chesbro (1957), Shewan (1959), Ingram and Thornley (1959), Thornley, Ingram, and Barnes (1960), and Phillips *et al.* (1961).

In order to obtain a useful extension of the storage life of fresh meat held at room temperature, when the predominant spoilage organism is no longer the radiation-sensitive

Pseudomonas, it is necessary to apply a much higher radiation dose.

Such treatments appear to be impracticable for various reasons: under aerobic conditions serious deterioration of fat may be expected, and under anaerobic conditions there is a danger of poisoning by *Clostridium botulinum*.

Some microbiological aspects of radiation-pasteurized meats requiring special attention are:

- The possible development of radiation-resistant strains (see, for example, Erdman, Thatcher, and MacQueen 1961).
- The subsequent mode of microbiological spoilage of radiation-pasteurized foods, which may differ from familiar patterns because the treatment has altered the balance of microbial flora present (see, for example, Ingram and Thornley 1959).
- Where pathogens such as *Cl. botulinum* may occur, the storage conditions necessary for adequate control of these organisms.

Wholesomeness

The radiation process cannot be used without the approval of the appropriate health authorities, and before this approval is given there has to be convincing evidence of the wholesomeness of irradiated foods. Because of the newness of the process and the complicated nature of the interaction of radiations with foods, the collection of such evidence is time-consuming. However, good progress has been made, and in February 1963, the U.S. Food and Drug Administration gave its clearance for unrestricted public consumption of bacon irradiated, in tin cans, with 4·5 million rads from a cobalt-60 source. This is the second clearance of an irradiated food given by a Western country, the first being for the marketing of irradiated potatoes in Canada. The U.S. Army hopes soon to receive clearance from the Food and Drug Administration for irradiated wheat flour, potatoes, canned chicken, fruit compote, oranges, and pork loins (Anon. 1963).

Radiation Methods

Two types of radiation suited for processing food are gamma rays from radioactive material and electrons from electron accelerators. For thinner samples, such as cuts of meat, either gamma rays or electron accelerators could be used, but for thick or dense samples, gamma rays have an advantage because of their greater penetration.

Important parameters for radiation processing are:

- The rate at which material has to be treated.
- The dose required.
- The amount of overdosing that can be tolerated.

The economics of processing by irradiation has been considered by the United Kingdom Atomic Energy Authority (1963). The cost varies with the application. For a dose of 2·5 million rads, costs estimates vary from 2·6 pence (sterling) per pound for a relatively large, efficient plant to 22·0 pence per pound for a smaller, less efficient plant. It appears that for a pasteurization dose of 50,000 rads, costs could be of the order of 0·1 to 0·2 pence per pound. As a radioactive source emits radiation continuously and cannot be switched off, it is very desirable to make maximum use of the plant.

Conclusion

Radiation sterilization is not expected to be of significance for meat preservation for civilian use in the immediate future. Radiation pasteurization is more promising, particularly where a modest increase in the refrigerated shelf life is of value. There can be no commercial use made of the process until approval of health authorities has been obtained; this is being actively sought in the United States and the United Kingdom.

Irradiation costs can be quite low and may represent only a small proportion of the cost of meats.

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Pale Watery Pork Muscle

By R. G. Cassens

Although pale watery pork muscle is well known in America and in Europe, little has been heard of it in Australia, possibly because it has not been recognized. Dr. R. G. Cassens, who had previously worked on the problem at the University of Wisconsin and recently returned to the U.S.A. after spending almost a year at the North Ryde laboratories of the CSIRO Division of Food Preservation as a Fulbright scholar, here summarizes some of the latest findings on the subject.

INTRODUCTION

Pale soft watery pork muscle, or "white muscle", is characterized by a pale colour, open structure, and excessive loss or exudation of fluid. The post-mortem changes that give rise to this condition occur in what may appear to be normal muscle at the time of death of the animal. The resulting meat not only lacks aesthetic appeal but poses a problem to the processor in that it possesses poor water-binding and emulsifying properties. The occurrence of pale watery pork is usually reported from observations of the longissimus dorsi and exposed ham muscles; these are the largest muscles of the carcass and the most valuable.

Distribution

The condition has been reported under different names in several countries. Ludvigsen (1954) used the term "Muskeldegeneration" to describe similar symptoms noted in Danish Landrace pigs, and his work revealed that the muscles had a low pH (5·3–5·5) soon after death. He suggested that a failure of the physiological mechanisms to respond adequately to stress was the cause. Lawrie (1960) has reported the disorder in England under the designation "white muscle disease" and noted that muscle so affected attains an extremely low ultimate pH. French workers (Henry and Billon 1955) have also described "exudative" muscle in pork, and the symptoms are well known in America, where, at the Wisconsin Agricultural Experiment Station, work has been completed on characteristics of muscles showing various degrees of paleness and wateriness (Briskey *et al.* 1959*a*). There have also been recent reports describing the condition in Ireland (McLoughlin and Goldspink 1963) and in the Netherlands (Hart *et al.* 1963).

There is practically no information concerning the disease in Australia, and it appears that no investigation has been conducted here to ascertain whether or to what extent it occurs in this country, although there is some indication that in fact it does.

Biochemical Changes in Muscle *Post Mortem*

Many of the biochemical changes related to or occurring with pale watery pork muscle have been elucidated, but the *in-vivo* conditions that induce the development of symptoms in a particular case appear to be extremely complex and are as yet unknown.

Normal muscle undergoes a series of well-known post-mortem biochemical changes. These are a lowering of the concentration of adenosine triphosphate (ATP), which is a normal component of living muscle, and a concomitant depletion of glycogen. The metabolic breakdown of glycogen results in the production of free lactic acid and there is a consequent lowering of the pH of the muscle. As the pH falls and the concentration of ATP approaches a limiting value, the muscle contracts and loses its extensibility, passing into the condition known as rigor

mortis. These events leading to the onset of rigor mortis are well known, but the underlying processes of rigor mortis and its subsequent resolution are little understood.

FACTORS AFFECTING APPEARANCE OF PORK MUSCLE

The fall in pH due to the liberation of lactic acid, the amount and characteristics of the muscle glycogen, and the onset of rigor mortis all determine the ultimate appearance of pork muscle; the rate of fall in pH and the rapidity of onset of rigor mortis appear to be particularly important.

pH Changes

Briskey and Wismer-Pedersen (1961) have distinguished four types of pH pattern:

- a slow, gradual decrease to 5·7–6·3;
- a gradual decrease to about 5·7 in 8 hr, with an ultimate pH of 5·3–5·7;
- a relatively rapid decrease to about 5·5 in 3 hr, with an ultimate pH of 5·3–5·6;
- a sharp, significant decrease to about 5·1 in $1\frac{1}{2}$ hr, and a subsequent increase to 5·5–5·6.

The first three types are associated with an acceptable product, but the fourth type yields pale exudative tissue with a soft, inferior structure.

Rate of Glycolysis

Several workers have shown that increasing the glycogen content of pork muscle results in a greater fall in pH and a higher incidence of pale watery muscle, and the structural characteristics of glycogen have also been investigated in this context. Sayre, Briskey, and Hoekstra (1963*a*) found that sucrose feeding tended to lengthen both the external and internal molecular chain lengths of muscle glycogen, whilst accelerating the rate of anaerobic glycolysis. Muscles of the Chester White breed showed a slow rate of anaerobic glycolysis, but during post-mortem glycolysis a more severe decrease in both external and internal molecular chain length of glycogen occurred with this breed than with Hampshire or Poland China breeds.

An interesting suggestion of Bendall and Wismer-Pedersen (1962) is that the sarcoplasmic proteins, that is, the non-fibrous intracellular proteins, are denatured and precipitated on the fibrillar proteins, and that this process results in the decreased water-binding capacity shown by pale watery pork muscle. They have suggested that the denaturation occurs because of the rapid rate of lactic acid production while the muscle is still at a relatively high temperature.

Time Factor in Rigor Mortis

Since the time course of rigor mortis is a result of the biochemical changes previously mentioned, it has been studied in relation to the ultimate appearance of pork muscle. Briskey, Sayre, and Cassens (1962) found that a rapid (10 min) or moderately slow (60 min) delay phase during acid rigor resulted in pale watery tissue, whereas normal tissue was associated with a short delay phase (30 min) and a moderately long onset phase, providing the pH of the muscle after 45 min remained high.

Bendall, Hallund, and Wismer-Pedersen (1963) have classified pork carcasses according to their muscle quality—the designation of carcasses as Group A indicated excellent quality, whereas those showing more or less watery muscle were classified as Group B. Group A muscle was characterized by a slow fall of pH (maximum of 0·65 pH unit/hr) and a slow decrease in extensibility (full rigor at 280 min). Group B muscle showed a rapid fall of pH (maximum 1·04 pH units/hr) and a rapid development of rigor (full rigor at 160 min).

Further studies on the relation between pork muscle colour and water-binding properties on the one hand, and the concentration of lactic acid and muscle temperature on the other, should prove valuable in furthering an understanding of the phenomena associated with these changes.

CONTROL METHODS

Several methods have been investigated for increasing or reducing the incidence of pale watery pork. Such variables as feeding regimen, pre- and post-slaughter handling practices, and breed may be important in determining the ultimate characteristics of the muscle.

The effect of sugar feeding is well known (Gibbons and Rose 1950; Wismer-Pedersen

1959; Briskey *et al.* 1959*b*). The general result is to increase the glycogen level and thereby depress the ultimate pH. In consequence, or because of the more rapid rate of fall in pH, the pork muscle is more liable to develop the pale watery condition.

Methods which deplete or lower the glycogen reserves in muscles of the living animal generally result in a higher ultimate pH of the carcass meat and darker-coloured muscle. Such treatments include exhaustive exercise, adrenalin administration, electric shock treatment, and pre-slaughter exposure to ice-cold water.

Exercise.—The effect of exhaustive exercise on pork muscle quality has been well substantiated (Briskey *et al.* 1959*c*), but it is important that the animal be exercised to complete exhaustion if the glycogen reserves are to be depleted adequately. If exercise is discontinued too soon, the only result is excitement of the animal, which may lead to rapid post-mortem glycolysis of the muscle and the production of the pale watery condition. This may occur, for example, when pigs being prepared for slaughter are allowed to become over-excited.

Adrenalin.—The immediate effect of adrenalin administration is to lower or deplete the glycogen supply, and this is reflected in the post-mortem pH of the muscle. The work of Radouco-Thomas *et al.* (1959) showed that the pH of normal hog muscle, initially about 6·8, may drop to 5·6 in the rigor phase; in adrenalinized hog muscle the pH remains at about 6·5.

Electric Shock.—Electrical stimulation has also been shown to lower the glycogen supply of muscle. Lewis, Brown, and Heck (1958) found that periodic electric shocks applied for five hours before slaughter significantly increased the pH of the longissimus dorsi, psoas major, and quadriceps femoris muscles.

Temperature.—It is known that pigs respond to fluctuations in environmental temperature, and there is a possibility that a decrease of glycogen reserves during cold weather accounts for a decrease in the incidence of pale watery muscle in pigs killed then. Accordingly, one method of reducing muscle glycogen is to expose the animals to an ice-water bath immediately before slaughter. Sayre *et al.* (1961), using this technique, confirmed the reduction in glycogen level of the muscle and noted that the muscles appeared generally firm and dry. Increasing the animal's temperature, however, results in an increase in the rate of post-mortem glycolysis, as indicated by a rapid fall in pH and a paler colour. These effects were found by Sayre, Briskey, and Hoekstra (1963*b*), who placed pigs in a controlled temperature chamber at 42–45°C for 20–60 min immediately before slaughter.

A practical consequence of the effect of temperature on the muscle is that during normal processing prompt removal of the carcasses to chiller temperature following dehairing and evisceration is important if the rate of glycolysis is to be kept low.

The preceding discussion serves to illustrate the variety of conditions that may be related to the development of pale watery muscle in pork. In what follows, two particular aspects of the problem, on which I have worked, are discussed. Full details and data have been published elsewhere (Cassens, Hoekstra, and Briskey 1963*a*, 1963*b*, 1963*c*, 1963*d*).

THE ROLE OF ZINC IN PORK MUSCLE

The first aspect investigated was the importance of zinc in pork muscle. Previous work on beef muscle by Swift and Berman (1959) had indicated that zinc content was associated with pH and water retention of the muscle. Their work was conducted on a series of eight different beef muscles, and it was found that the muscles with the highest zinc content had a high ultimate pH and high water retention. In view of this information, we at Wisconsin undertook to ascertain the zinc level in the same eight muscles in pork and to determine if differences in the zinc content of the various muscles could be related to the differences in muscle function, myoglobin concentration, post-mortem pH, and post-mortem expressible water. This approach to the problem of soft watery pork muscle merited investigation because of the possible association of zinc with pH and water-binding capacity.

The table lists the eight muscles studied and gives the zinc contents, 24-hr pH values, and myoglobin concentrations found. The data illustrate the large differences which exist in zinc content, pH, and myoglobin content in different but sometimes adjacent muscles of an animal. They also indicate the errors which may be involved in extrapolating to the entire muscle mass of an animal body analytical data obtained from a single muscle. It is interesting to note that the low-zinc, low-myoglobin muscles are generally the least active, serving more of a tetanic function than the darker-coloured, high-zinc muscles, which can be considered to be in a tonic state of activity most of the time.

Characteristics of Eight Porcine Muscles*

	Zinc†	pH‡	Myoglobin§
Longissimus dorsi	69	5·46	3·92
Psoas major	87	5·56	7·43
Semimembranosus	98	5·57	5·92
Latissimus dorsi	130	5·63	6·46
Semitendinosus	139	5·67	7·78
Rectus abdominus	217	5·98	10·00
Trapezius	230	5·77	12·51
Serratus ventralis	247	5·88	13·91

* Zinc and pH expressed as average value from 16 animals and myoglobin expressed as average of 8 animals.

† Expressed as p.p.m. on fat-free dry basis.

‡ 24 hr *post mortem*.

§ Mg of myoglobin per g of fat-free dry tissue.

Statistical analysis divides the eight muscles in the table into three groups on the basis of zinc content. The muscles of high zinc content are usually dark, firm, and dry when removed from the carcass 24 hr after death; but the low-zinc-content muscles (longissimus dorsi and semimembranosus) are paler, have a lower pH, and are most frequently associated with the pale watery condition previously described.

Expressible water values for the eight muscles were determined by the filter paper press technique of Grau and Hamm, as modified by Briskey *et al.* (1960). "Within-muscle" correlations of zinc content with expressible water were both positive and negative, with a low total correlation. Some difficulty was encountered with this method of determining expressible water owing to the high fat content of some muscles.

It is easy to see, when the average figures are considered for each of all eight muscles, that a high association exists between zinc content and pH or myoglobin content. The muscles with a high average zinc content are those which also attain a high ultimate pH and have a high average myoglobin content. However, for the limited number of animals included in this experiment, "within-muscle" correlations between zinc content and pH or myoglobin were not statistically significant.

These findings prompted another experiment with 36 animals, comprising equal numbers of Hampshires, Chester White, and Poland China breeds, from which only two muscles (longissimus dorsi, representing low-zinc-content muscle, and trapezius, representing high-zinc muscle) were examined, in order to ascertain whether there was in fact a "within-muscle" relationship connecting zinc content and pH. The experiment also encompassed the response of the two muscles to pre-slaughter sucrose feeding, short-term excitement and exercise, fasting, and, of course, breed.

Figures 1 and 2 illustrate the pH and colour change of the two muscles during the first 24 hr *post mortem*. Colour is indicated in terms of reflectance values, a higher value corresponding with a lighter or paler colour. The trapezius muscle contained three times more zinc and myoglobin than the longissimus dorsi muscle, and although the pH of both muscles shortly after slaughter was 6·4, the pH of the longissimus dorsi fell much faster and to a greater extent than that of the trapezius; likewise, the colour change was faster and of greater magnitude. "Within-muscle" correlations between zinc content and 24-hr pH were, however, low and non-significant.

The excitement and exercise applied in this experiment constituted a stress factor and were found to lower the initial pH of the longissimus dorsi muscle as well as to induce a more rapid colour change. The trapezius muscle did not respond to the same degree.

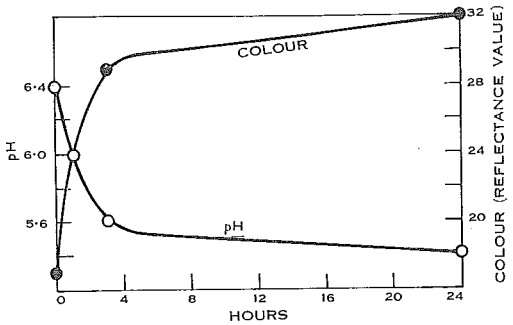


Fig. 1.—Post-mortem properties of the longissimus dorsi muscle. Zinc, 69 p.p.m. on fat-free dry basis; myoglobin, 3·65 mg/g fat-free dry tissue.

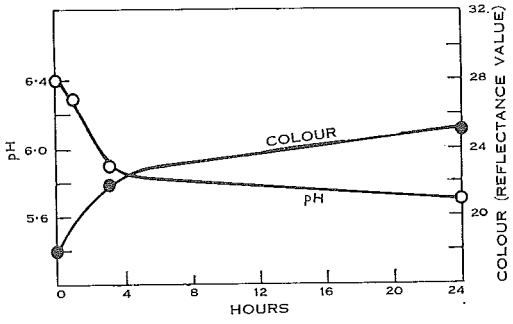


Fig. 2.—Post-mortem properties of the trapezius muscle. Zinc, 183 p.p.m. on fat-free dry basis; myoglobin, 10·76 mg/g fat-free dry tissue.

Neither breed nor sucrose feeding affected the zinc or myoglobin content of either of the two muscles, which differed widely in their content of these materials.

Conclusions which may be drawn from these investigations on zinc in pork muscle may be summarized as follows:

- Pork muscles differing in location and possessing a different function and different post-mortem properties differ in zinc content as much as threefold.
- Groups of muscles of high zinc content exhibit, on the average, a high myoglobin content, but within the same muscle there is little connection between zinc content and ultimate pH or myoglobin content.
- The zinc content of a high-zinc muscle (trapezius) or of a low-zinc muscle (longissimus dorsi) was not affected by breed, pre-slaughter sucrose feeding, short-term excitement and exercise, or fasting, even though these factors could alter some post-mortem properties of the muscle.

ELECTRON MICROSCOPE STUDIES

Many studies of muscle by means of the electron microscope have been reported, but these have been concerned mainly with preserving and studying the muscle in as near the living state as possible. The object of the studies now described was to follow structural changes during the first 24 hours after death, particularly those produced by a rapid rate of glycolysis. The investigation was designed to detect any major structural changes which might be linked with the development of the pale and watery condition typical of the disorder under consideration. Changes in the myofibrils and sarcoplasmic components may be followed by means of the electron microscope but are not generally visible under the light microscope.

The most marked change found in normal pork muscle *post mortem* was a disruption of the sarcoplasmic components. This disruption occurred rather slowly and often even up to four hours after death little change could be detected. But by 24 hours the sarcoplasmic space appeared to be almost free of granular or membranous material, except for a few mitochondria.

Effect of Temperature Environment

In further studies, pigs were confined in a controlled high-temperature chamber, as described by Sayre, Briskey, and Hoekstra (1963*b*). Figures 3–5 illustrate muscle from a pig which had been subjected to such treatment and whose muscle temperature reached 46°C (115°F) at the time of death. Twenty-four hours later the muscle was extremely pale and was exuding large quantities of fluid.

Figure 3 shows the muscle immediately after death of the animal and indicates the large number of mitochondria present. The muscle appears to be contracted, as evidenced by the narrow *I* bands.

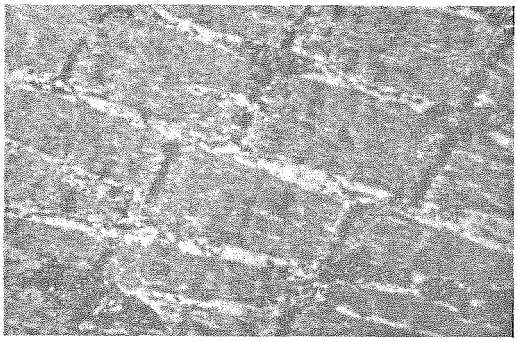


Fig. 3.—Electron micrograph of pork muscle immediately after death, showing mitochondria and *I* bands.

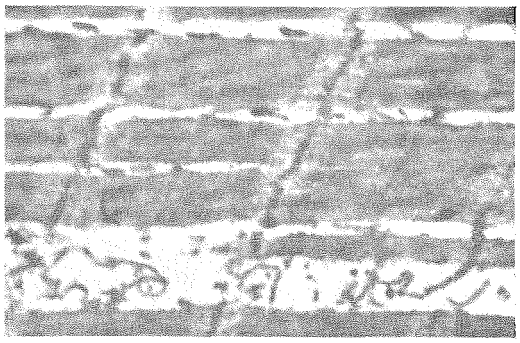


Fig. 4.—Electron micrograph of the same muscle 15 min after death at the onset of rigor mortis, showing disruption of sarcoplasmic components.

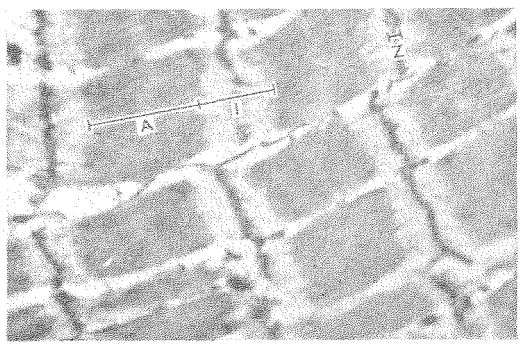
Figure 4 shows the same muscle only 15 minutes later. The pH was already down to 5·6 and rigor mortis was setting in. In this instance of extremely rapid glycolysis a very rapid disruption of sarcoplasmic components was occurring, as may be seen by comparing this micrograph (Fig. 4) with the earlier one (Fig. 3).

Figure 5 shows the muscle 24 hours after death. The significant point is the change in appearance of the *A* bands, which are granular instead of being filamentous, as they normally are because of the alignment of myofilaments. This suggests that the myosin filaments have broken down, possibly owing to the extremely rapid rate of glycolysis at the elevated temperature. A disruption of this nature may be important in the loss of water-binding capacity usually noted in affected muscles.

A different situation develops if the pig is first heated in the high-temperature chamber and then subjected to an ice-cold bath (Kastenschmidt, Briskey, and Hoekstra, unpublished data, 1962). Figure 6 illustrates a 24-hr post-mortem muscle sample from a pig treated in such a manner. In this case the onset of rigor mortis was very rapid, occurring only 20 minutes after death, but at a high pH of 6·6. The 24-hr pH was 5·9, the muscle appeared normal to dark in colour, and when the surface was cut it did not exude fluid. The electron micrograph shows the myofibrils in an excellent state of preservation.

Fig. 5.—Electron micrograph of the muscle shown in Figures 3 and 4, 24 hr after death, showing disruption of *A* bands. Visually this muscle was pale and it was soft and watery.

Fig. 6.—Muscle 24 hr after death of a pig overheated and then chilled in ice immediately before slaughter, showing normal fibrillation, *A* and *I* bands, and *Z* line. Visually the muscle appeared moderately dark and it was dry and firm.



Contraction Bands

During the course of the electron microscope studies "contraction bands" were also observed and studied. Contraction bands have been known for some time, and may be produced by substances causing a violent contraction of the muscle. In this study they were observed only occasionally, in samples taken immediately after the animal was killed. They are thought to have arisen from a strong contraction undergone because of some stimulus during removal and initial fixation of the sample.

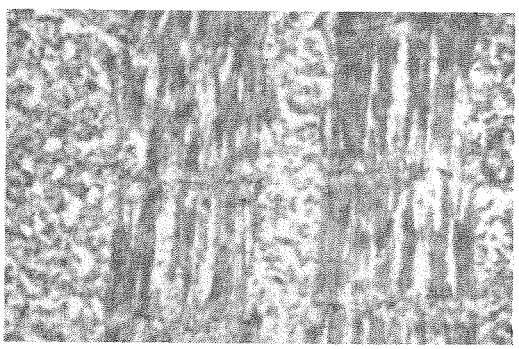


Fig. 7.—Electron micrograph showing appearance of dense, irregularly banded material (contraction bands) in porcine muscle fibres.

Whether these contraction bands correspond to the material described by Bendall and Wismer-Pedersen (1962) in 24-hr-old samples is not known. They ascribed the origin of their material to a precipitation of sarcoplasmic proteins on the myofibrillar proteins, but material here observed (Fig. 7) is seen to be continuous with the myofibrils, as evidenced by its filamentous appearance. It may also be noticed that the sarcoplasmic spaces are packed with granular material and that there seems to be a lack of membranes. The relation of such material to the problem of soft watery pork muscle needs further investigation.

CONCLUSION

From what has been said, it should be clear that the elucidation of the causes and mechanism of the development of the pale watery condition in pork muscle is not yet complete. Nevertheless, some progress has been made in defining some of the causative factors and in recognizing associated changes in the muscle. From the electron microscope studies it may be concluded that whereas in normal muscles undergoing post-mortem glycolysis a slow disruption of sarcoplasmic materials occurs, affected muscle behaves differently. Thus in muscle undergoing rapid post-mortem glycolysis in which rigor mortis sets in rapidly at low pH—a combination of factors associated with the development of pale watery muscle—there is a rapid disruption of sarcoplasmic material and some damage to the myofibrils. It is possible that such myofibril damage has an important bearing on the water-binding properties of the muscle and on the consequent exudation of fluid typically associated with the pale watery condition of affected pork muscle.

Pale watery pork does not appeal to the eye and is not readily accepted by the consumer. If used in manufacturing processes it may give undesirable results, particularly militating against attainment of the high degree of standardization of the product which is nowadays usually required.

Whilst the incidence of the disorder may be reduced by correct management practices in the feeding, handling, and slaughtering of pigs, a final solution of the problem requires a continued attack from the fields of muscle biochemistry, histology, genetics, and animal physiology.

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Bacterial Greening of Smallgoods

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ADVANCES of science and technology in modern times have brought to the public a large range of convenience foods, which include pre-packaged fresh meats and packaged cooked sausage meats. These and similar convenience foods have associated with them many microbiological problems, the most important of which is economic loss due to microbial spoilage, whether this occurs at the processing plant, the retail outlet, or in the household refrigerator.

With cured smallgoods the presence of salt and certain other ingredients inhibits bacteria that normally cause spoilage of uncured meats. However, such cured meat products act as selective media for lactic acid bacteria, micrococci, yeasts, and moulds; spoilage can still occur, although normally it takes a different form from that occurring in uncured meats.

In this short article it is proposed to consider only a particular type of bacterial spoilage of cured meats, recognized by the development of a green discoloration. "Greening" is the term used to describe the green discoloration found in some spoiled cooked cured meats; it can be found in rings in sausage material, in the core of sausage products, or on the surface. Bacteria are usually, but not always, associated with these areas of green discoloration but when present they can be isolated in pure culture, and on re-inoculation to uncontaminated material they produce a typical discoloration.

The green discoloration is a product of the reaction between peroxide produced by bacteria in the presence of oxygen and the pigment of the cured meat. It may develop only on exposure of the material to oxygen, and it should be borne in mind that aged material may have a large bacterial population without visible discoloration. Such greening may occur only after the consumer has opened a package.

Types of Bacterial Greening

As indicated above, bacterial greening can be divided into three types on the basis of where the greening occurs.

Green Rings.—A ring appears at varying depths beneath the surface, and can be seen as soon as the sausage is cut. It usually develops 12 to 36 hours after processing, even under adequate refrigeration. Although bacteria may have been present throughout the sausage, the discoloration develops in a ring or annular form probably because only in this zone are the oxygen tension and other factors conducive to the oxidation of the pigment. The defect is associated with an unusually high population of bacteria in the sausage mix before processing. Even though the bacteria may have been killed in the heat processing, the damage has been done by that time, although it may not be apparent.

Green Cores.—With this type of greening, the centre of the sausage is discoloured. This is usually caused by an excess of nitrite or by lactic acid bacteria. Discoloration due to excess nitrite is more common in fermented-type products and can be seen at the time of cutting the sausage. The bacterial type of discoloration usually occurs in products of large cross section; discoloration is not visible at the time of cutting, but only becomes apparent one to several hours later. The cause of this type of bacterial greening is an inadequate heat treatment leaving viable "greening" bacteria in the centre of the sausage. This is followed by growth of these surviving organisms. Usually a minimum of four days under normal storage conditions is needed before spoilage can be detected. The sausage will appear normal externally, but, on cutting, the green discoloration develops. It rarely penetrates more than one-eighth of an inch from the cut surface, and the retailer may be led to believe that the spoilage is confined to this surface. Actually it is throughout the sausage and will reappear after several hours as new surfaces are exposed.

Surface Greening.—This type of greening is the most common. It results from contamination of the meat after heat processing, followed by holding conditions that allow extensive growth of the contaminating greening bacteria. Material cooked in impermeable membranes which are not broken should not show surface greening. However, the removal of casings or slicing or repackaging can recontaminate the product with a wide variety of microorganisms.

How to Ascertain if Greening is Bacterial

Since a green discoloration on cured products may be caused by agencies other than bacteria, even apart from accidental staining (e.g. by metals), it is desirable that a simple technique should be available which permits positive confirmation of the presence of viable bacteria capable of causing greening. The following two tests can be used.

Confirmatory Test.—Place a slice of freshly cooked sausage material on top of moistened blotting-paper in the bottom of a screw-topped jar. Steam the jar for 30 minutes or pressure cook for an equivalent time (approx. 10 lb/sq in pressure for 10 min). Smear the surface of some of the fresh product with a scraping from the green area of the discoloured product, and incubate the jar in a warm room (68–86°F) overnight.

It is advisable that a "control" be run concurrently with the test, this being treated in an identical way except that the surface is not smeared with the suspect material. The smeared material should show typical discoloration, whilst the "control" should show no visible changes.

Isolation of Bacterial Colonies.—A laboratory test for isolation of the causal agent involves the use of manganese dioxide–APT agar medium. Manganese dioxide (7·5 g) is added to 50 ml of water and autoclaved, e.g. in the pressure cooker. The suspension is mixed and 2 ml is added to 100 ml of "Difco" APT agar.* A Petri dish is poured with ordinary APT agar and after this has set a thin layer of manganese–APT agar is poured over the original APT agar. A scraping of the green material is streaked on the surface of the agar, and the Petri dish incubated at 30°C (86°F) for 48 hours.

Catalase-negative bacteria will give a zone of clearing around the colony. Individual colonies of this type may then be tested by inoculation onto meat as in the confirmatory test described above.

Preventive Measures

When greening has been demonstrated to be bacterial in origin, any points at which gross contamination might occur before, during, or after processing or during storage and distribution of the product should be looked into. Also it may be advisable to check whether processing conditions, temperature control, and storage facilities are adequate to prevent or inhibit the development of bacteria.

Almost certainly, stricter control of hygiene in all phases of preparation, careful control of temperatures, and the use of only freshly slaughtered meat will result in a product less likely to be affected. Cooking, provided due regard is given to the maintenance of an adequate internal temperature for sufficient time (e.g. 150–155°F for at least 10 min), will destroy most of the bacteria present in cured meats. Bacterial spores, which are relatively heat-resistant, may not be killed under these conditions, but since spore-forming bacteria cannot grow easily at temperatures close to 32°F, their development may be prevented by rapid cooling immediately after cooking, followed by refrigeration.

Smallgoods made from fresh material enclosed in a water-impermeable membrane that have been cooked adequately and cooled rapidly thereafter before being stored at a low temperature (32°F) will normally have a storage life of at least two months. Where the product is sliced or cut up, recontamination can occur, and in the handling of such material, in regard to both repacking and distribution, particular attention must be paid to cleanliness of equipment and personnel and to adequate refrigeration of the product during storage and transport.

* EVANS, J. B., and NIVEN, C. F., JR. (1951).—Nutrition of the heterofermentative lactobacilli that cause greening of cured meat products. *J. Bact.* **62**: 599.

Science and Industry Day, 1963

DELEGATES from the food industry were welcomed by Dr. S. H. Bastow, a member of the CSIRO Executive, to a display in the Food Processing Area of the CSIRO Division of Food Preservation at North Ryde on the afternoon of Monday, November 18.

Among the several exhibits was a belt trough dryer recently installed for experimental work. This machine, the installation costs of which had been met from funds donated by the Australian food industry, was shown in operation with a charge of diced carrots.

Other equipment on display included an experimental model demonstrating the principle of fluidized-bed techniques, these being applicable to the freezing and drying of various foods. A small freeze-drying unit was also on show, together with samples of freeze-dried and dehydrated foods and technical data relating to the operating characteristics of freeze-drying processes. Recent work by the Division on the properties and application of flexible film for packaging foods was illustrated in one display bay, and in another were samples of frozen fruit and vegetables. Problems which arise in connection with the handling, storage, and transport of fresh fruits in fibreboard cartons and in bulk bins were also illustrated.

Discussions on Industry Support

The Chief of the Division, Dr. J. R. Vickery, later invited discussion on mutual collaboration between the food industry and CSIRO. He said that one of the major aims of CSIRO was to encourage industry to undertake research and development, especially when the industry was a large one, since obviously CSIRO could not undertake to solve every firm's individual problems. If more was to be done by this Organization for the food industry, the industry itself must be prepared to contribute financially and otherwise. He suggested that even small firms, or those with limited sectional interests, might with advantage to themselves contribute to existing organizations carrying out research in their fields, such as the Australian Bread Research Association, the CSIRO Division of Dairy Research, and the CSIRO Division of Food Preservation.

Referring to the work of his Division, Dr. Vickery said that costs were soaring and he estimated that it now cost about £11,000 per annum for each research worker, allowing for services and facilities that must be provided. The result had been a squeeze on funds for equipment, and he was grateful for the contributions made by the food industry towards the cost of purchasing and installing certain experimental machinery. This had enabled work to be done on problems which otherwise could not have been tackled at this stage.

Dr. Vickery said that several years ago he estimated that the annual savings accruing to the food industry as a result of completed CSIRO research were about £600,000, and he thought that the figure would now be much higher; for example, the pea maturometer was estimated to be saving canners £100,000 annually, and work on citrus wastage had resulted in savings estimated at £70,000 per annum.

In the ensuing discussion Mr. V. Heine (John Heine & Co. Pty. Ltd.) said that as a builder of food machinery he envied the canners in that when they ran into technical difficulties they could turn to Dr. Vickery and his staff of expert scientists and technologists for assistance and advice. But should not the whole food industry, which would ultimately benefit, collaborate in some sort of collective effort similar, for instance, to the Products Engineering Research Association of Great Britain? In 1962 that organization dealt with more than 3000 problems at a total cost of £589,000 which was borne entirely by industry.

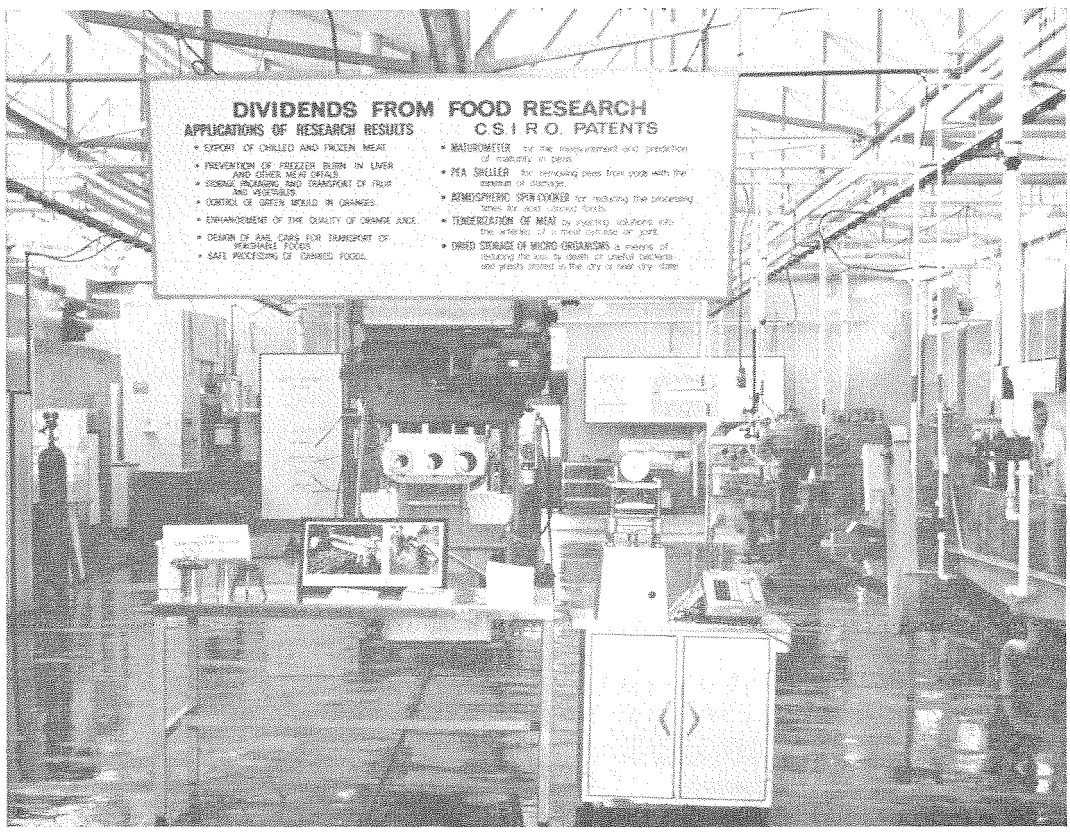
Other speakers considered that the food industry was too diversified to support a research association of its own, even allowing for the CSIRO subsidy which would be forthcoming if one were formed. Although in Great Britain the whole industry was well catered for by only two such research associations, many speakers stated

that under Australian conditions it was preferable to support existing organizations, such as those of CSIRO. Perhaps, however, CSIRO was making some of its work available too freely to those who were contributing nothing, and should institute service charges for certain facilities such as taste testing.

The point was made that several firms might be more ready to utilize CSIRO research facilities if they could be assured that the results of work carried out at their request were kept confidential to themselves. In reply Dr. Vickery pointed out that over 90% of the Division's funds were derived from Government sources and since this was public money CSIRO was obliged to make its results available to all who were genuinely interested. Dr. Bastow, speaking for the Executive, emphasized, however, that any firm which had a production problem considered to be of general interest to the whole industry could count on the wholehearted collaboration of CSIRO in attempting to find a solution. While the company might not have exclusive rights on any solution worked out by the Organization it could gain a definite advantage over its less cooperative rivals through having collaborated from the start and because of the "know-how" acquired during the course of the investigation. Both individual firms and the industry at large had much to gain from collaborating with CSIRO in this way.

In summing up the discussion, Dr. Vickery said that it was clear CSIRO must still take the lead in tackling industrial problems requiring research, but it was also evident that the Australian food industry was becoming increasingly aware of the advantages of supporting such work.

A view of part of the Food Processing Area prepared for the display.



Conferences on Meat Research

IN the first week of September 1963 the CSIRO Division of Food Preservation held a conference in Brisbane, which was attended by representatives of the beef export industry and various State and Federal Government bodies, and delegates from meatworks throughout Australia. The purpose of the conference, at which the Division was strongly represented by research and other staff from its Meat Research Laboratory at Cannon Hill, Qld., and from its North Ryde headquarters, was to present some results of research work done within the Division and to discuss some of the technical problems of the industry. The main aim, however, was to give delegates the opportunity to express views on the relevance of current and proposed research programmes to the present and future needs of the beef industry.

Subjects of discussion and of papers read at the conference included methods of carcass appraisal and the graziers' and meat processors' approach to the question of defining meat quality; bacterial and other aspects of meat hygiene; and the organization of research relating to the meat industry.

The conference ended on the second day with a formal resolution calling for the setting up of an *ad hoc* committee to be convened by the Chief of the CSIRO Division of Food Preservation, Dr. J. R. Vickery. This committee, which would be known as Meat Industry Research Advisory Committee, would make recommendations on research proposals, advise on priorities, and generally serve as a technical liaison body between the meat industry and CSIRO. It would, however, be a purely advisory body and would not determine the allocation of research funds.

A few weeks before the Brisbane conference a two-day meat research conference was held by research officers of the Division at North Ryde, this also being attended by research staff from Cannon Hill. This conference was in the nature of a research symposium and the papers presented were of a highly specialized character, relating principally to muscle biochemistry, the properties of proteins, and the response of microorganisms to environmental factors.

Retorting of Canned Foods

THE National Canners' Association of the United States of America has assembled an audio-visual teaching aid intended to assist canners in the training of retort operators. It covers the essential theoretical and practical aspects of the retort processing of canned foods and the potential hazards involved. The teaching aid presents this information in a simple, direct manner which may be readily understood by persons not having special training.

The audio-visual kit comprises 71 2 in. by 2 in. colour slides and a 40 min $3\frac{3}{4}$ in. per sec tape recording. In addition the kit contains a discussion guide with a list of questions for the use of the instructor or discussion leader and a copy of the following N.C.A. Bulletins: 26-L, "Processes for Low-Acid Canned Foods in Metal Containers"; 30-L, "Processes for Low-Acid Canned Foods in Glass Containers"; and 32-L, "An Information Bulletin on Retort Operation".

The CSIRO Division of Food Preservation recently acquired one of these kits, which may be borrowed by Australian canneries for short periods for training purposes. Arrangements for borrowing the kit should be made with Miss B. Johnston, Librarian, CSIRO Division of Food Preservation, Box 43, Post Office, Ryde, N.S.W., or by telephoning Miss Johnston at 88 0233 (Sydney).

NEWS FROM THE DIVISION OF FOOD PRESERVATION

MEAT RESEARCH

Dr. W. J. Scott, Assistant Chief, has been appointed Leader of Meat Research in the Division. He retains his position of Assistant Chief, but he will now supervise the work of the Meat Research Laboratory (Brisbane) and the muscle biochemistry and physiology studies being conducted in Sydney. He will also maintain close liaison with the investigations on muscle proteins being carried out by Dr. R. W. Burley at the University of Sydney. For the time being Dr. Scott will remain at North Ryde, but it is expected that he will later transfer to Brisbane. His place as Senior Microbiologist in the Division has been taken by Dr. J. H. B. Christian.

TRAINEES FROM ASIA

Mr. Ryung Huh, a graduate in chemical engineering from the Seoul National University, Korea, who reached Australia in September 1963 to study food technology under the Korean Training Scheme, will have spent about 12 weeks with CSIRO, at the Division of Food Preservation, North Ryde, and at the Tasmanian Regional Laboratory, when he leaves Australia in April 1964. Mr. Ryung is a Planning Officer in the Sam Yang Company, Seoul, which processes foods of marine, plant, and animal origin. In Australia he is visiting many food production plants and studying the refining of sugar and salt.

Mr. M. S. Laul, a graduate in chemical engineering from the Institute of Technology, Nagpur, India, spent a short time in the Division studying the storage and handling of fresh fruit and vegetables, a number of aspects of the technology of canned foods, including the technology of tinplate, and investigations on food flavour. Mr. Laul is a Marketing Development Officer in the Indian Ministry of Food and Agriculture at Nagpur, where he enforces quality control regulations pertaining to fruit and vegetable products and has the task of developing the fruit and vegetable preserving industry on modern scientific lines. In the course of a six months' sojourn in Australia, ending in March 1964, Mr. Laul will have visited a large number of food processing plants and studied the manufacture of tinplate and food machinery.

MODERN TECHNIQUES FOR FOOD LABORATORIES

The CSIRO Division of Food Preservation has arranged for a series of talks and demonstrations to be given by members of its staff at the Food Preservation Laboratories, Delhi Road, North Ryde, on Wednesday, July 8, 1964. Under the general title "Modern Techniques for Food Laboratories", the talks will cover the subjects of gas chromatography, thin layer chromatography, the measurement of temperature and humidity, and microbiological techniques. Details will be sent to food firms shortly.

RESEARCH GRANTS FROM U.S.A.

The Foreign Research and Technical Programs Division of the U.S. Department of Agriculture has made two grants to the Division of Food Preservation under the Agricultural Trade Development Assistance Act 1954, generally referred to as Public Law 480.

The larger grant (£A46,000 over five years) is towards the cost of an investigation into the cyclopropenoid compounds which are found in cottonseed and cottonseed products. The presence of these compounds in rations fed to hens causes abnormalities in the eggs laid, namely, a pasty consistency in the yolks and the development of pink whites in stored eggs. The compounds also reduce the hatchability of fertile eggs and when ingested

in large amounts cause the hens to cease laying. The investigations, which will complement work being carried out in the U.S.A., will be concerned with the chemistry of the cyclopropenoid compounds and their biological effects. The results will be of considerable interest to poultrymen in Australia, where cyclopropenoid compounds are ingested by hens feeding on plants of the order Malvaceae, to which the common mallow weeds belong, because cottonseed may become an important commodity in Australia.

The smaller grant (£A8200 over three years) is for a study of the differences in the chemical structure of albumin, the principal protein of egg white, and S-ovalbumin, a more stable form (discovered by research workers in the Division of Food Preservation) to which it changes spontaneously during storage of the eggs. S-ovalbumin is indistinguishable from normal ovalbumin except for its resistance to denaturation by heat or chemical agents, but its formation probably accounts for the decline in the functional properties (especially the baking and whipping qualities) of the egg white, which has been studied extensively by scientists of the U.S. Department of Agriculture.

The Charles F. Kettering Foundation, Ohio, U.S.A., has made a grant of $18,500 (£A8200) to Dr. Robert M. Smillie, leader of the joint Plant Physiology Unit operated by the University of Sydney and the Division of Food Preservation. The grant is for the purchase of equipment for Dr. Smillie's research on photosynthesis.

International Food Industries Congress and Exhibition

THE publishers of the British technical journal *Food Manufacture* are organizing an international exhibition of food processing equipment and materials, and a congress on the practical aspects of food manufacture, to be held at Earls Court, London, June 8–12, 1964.

The exhibition, at which the many and varied needs of food processors will be on display, will be open to technical and business executives from the food industry and to the delegates to the congress, but not to the general public.

At the congress, for technical personnel from the food processing and related industries, papers on the practical aspects of modern food technology will be presented.

Inquiries concerning the congress and exhibition should be directed to the organizers at The Tower, 229 Shepherds Bush Road, Hammersmith, London, W.6.

Publications

REPORT OF FAO/WHO EXPERT COMMITTEE ON MEAT HYGIENE

Current emphasis on the introduction and maintenance of strict hygiene in Australian slaughterhouses and meatworks concerned with the preparation of boneless beef for export to the U.S.A. makes the Second Report of the Joint FAO/WHO Committee on Meat Hygiene* of particular interest at

* Joint FAO/WHO Committee on Meat Hygiene (1962) Second Report (Wld. Hlth. Org. Tech. Rep. Ser. 241: FAO Agricultural Studies No. 58). (Price: 6*s* 9*d* post free, from R. W. Barclay, 90 Queen St., Melbourne, C.1.)

the present time. This comprehensive report merits attention by all concerned in the handling and processing of meat, and rightly stresses the need for strict enforcement of adequate measures covering hygienic handling of animals from the farm and of meat through the abattoir and until it is consumed.

The report contains sections dealing with principles and objectives of meat hygiene; types of control which should be exercised; the classification of the principal diseases caused by meats; pre-abattoir handling of livestock; the design, construction, and operation of abattoirs; the inspection of meats, their manufacture, and their transport; the sanitation of retail shops and of "bulk feeding" kitchens; laboratory services and methods; establishment of standards for processed meats; the hygiene of meat handlers; special problems of meat hygiene; and new developments. To round off its report the Committee has listed problems which merit further investigation, including those concerning manufactured meats, where there are ample opportunities for bacterial growth if vigilance is relaxed.

In recognition of the rapid growth in many countries of the poultry industry, a special section has been devoted to the subject. In it the Committee suggests that the use now being made of dehydrated poultry products justifies extensive bacteriological studies.

Wherever it appeared desirable, the Committee has expressed opinions on vexed questions; for instance it considers that pending further investigations, the feeding of hormones to meat animals should be abolished or at least limited to preparations which are rapidly eliminated from the body.

The annexes to this very readable report include data relevant to its contents, the design of abattoirs, outlines of inspection procedures, regulations of various kinds, and a great deal of other information of value to the meat handler and processor. For a publication of some 90 pages, moderately priced at 5*s* sterling, the report is surprisingly comprehensive in coverage. Those engaged in the management of abattoirs and meatworks would be well advised to read it and to make copies available to members of their supervisory staffs. H.H.

RECENT PUBLICATIONS OF THE DIVISION

Copies of these publications may be obtained from the Librarian, Division of Food Preservation, Box 43, P.O., Ryde, N.S.W. (Tel. 88-0233.)

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MARSHALL, BETTY J., MURRELL, W. G., and SCOTT, W. J. (1963).—The effect of water activity, solutes, and temperature on the viability and heat resistance of freeze-dried bacterial spores. *J. Gen. Microbiol.* **31**: 451–60.

MIDDLEHURST, J., and KENNETT, B. (1963).—Flame ionization detectors. *J. Chromatogr.* **10**: 294–302.

MONTGOMERY, W. A., and PRATER, A. R. (1963).—Fisheries products. Fish sausages. Parts 1, 2, 3, 4. *Fish. News Lett. Aust.* **22**(3): 20; **22**(4): 25; **22**(5): 21; **22**(6): 19.

WARTH, A. D., OHYE, D. F., and MURRELL, W. G. (1963).—The composition and structure of bacterial spores. *J. Cell Biol.* **16**: 579–92.

WARTH, A. D., OHYE, D. F., and MURRELL, W. G. (1963).—Location and composition of spore mucopeptide in *Bacillus* species. *J. Cell Biol.* **16**: 593–609.