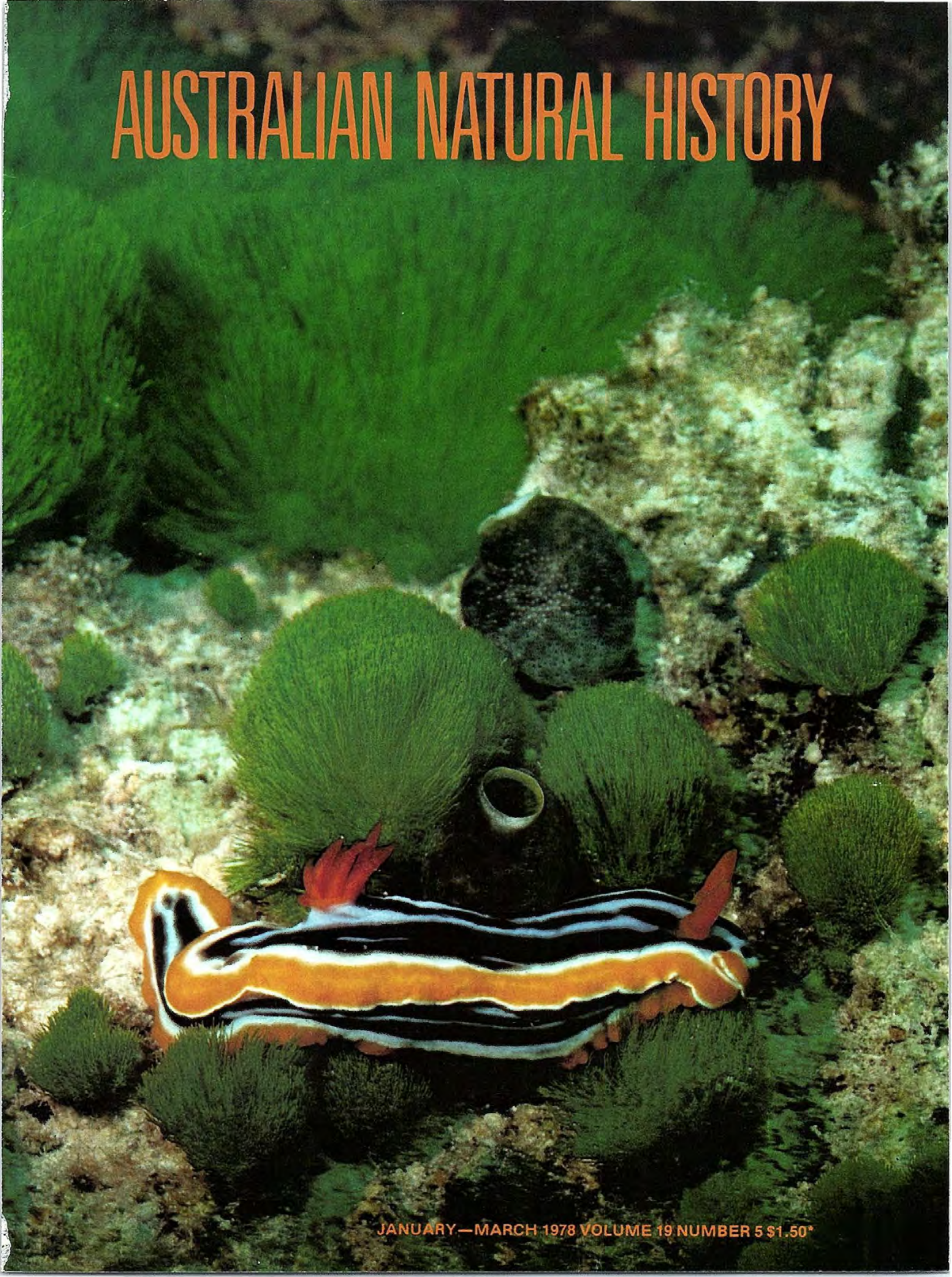
AUSTRALIAN NATURAL HISTORY



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AUSTRALIAN NATURAL HISTORY

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A Rotinese weaver works on an *ikat* cloth at her handloom.

COVER: A Nudibranch (*Chromodoris quadricolor*) exhibiting brilliant warning colouration. (Photo: Valerie Taylor).

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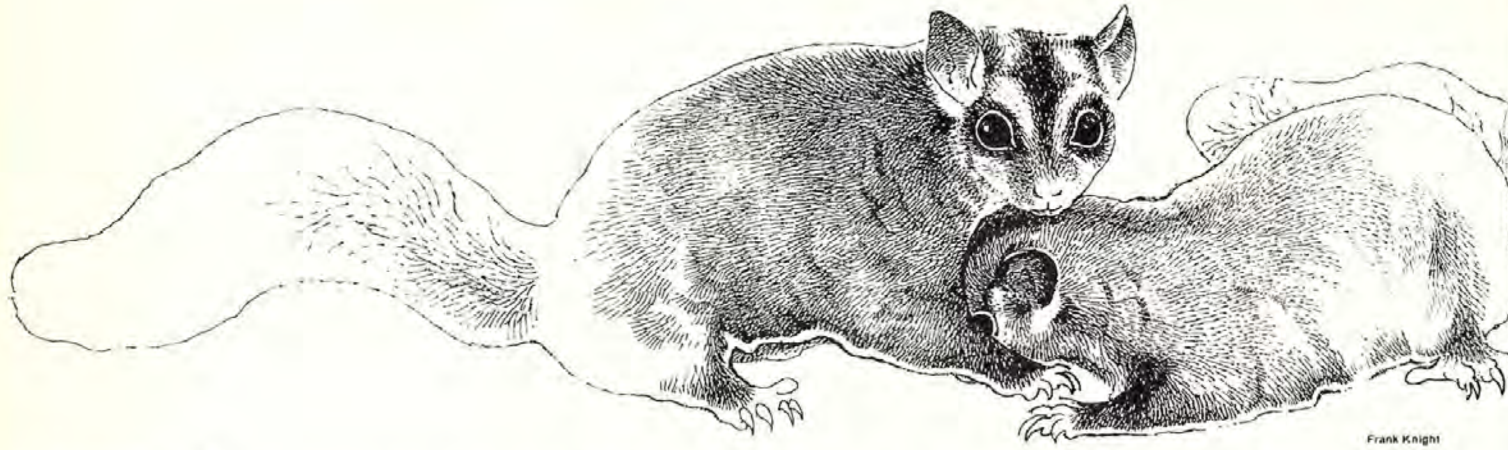

A sugar glider, *Petdurus breviceps*, marking a conspecific with the secretion from a gland situated on its forehead.

To communicate with members of their own and other species, animals, like man, rely on sight, sound and touch as well as on taste and smell. Chemical communication through taste and smell is particularly advantageous for those species which live in darkness or where silence is desirable. In animals, odour-messages are the equivalent of our written language since they function even in the absence of the individual sending them and can be long-lasting.

Scientific interest in olfaction (smell) began about forty years ago. It has increased considerably since then due to three main factors. Firstly, it was found that the nervous impulses in olfactory systems could be recorded electrophysiologically. Secondly, the evolution of modern electronic technology gave chemists a range of tools, which enabled them to study materials available in only milligram or even microgram amounts. Finally, a strong impetus resulted from a tremendous growth in ethology—a new branch of the biological sciences dealing with comparative studies of behaviour—which revealed clearly the need for animals to communicate with one another and with their environment.

It is not the purpose of this article nor is it possible, to paint a complete picture of the role of odour in the life of animals. Only a few examples are presented here to highlight the methods of silent communication in different classes of animals.

It is proper to start with insects since at this stage their olfaction is best understood. Entomologists who pioneered this field of work introduced the term 'pheromone', which is now so eagerly and frequently used and misused in references to the behavioural function of smell. The word is derived from the Greek *pherein* (to transfer) and *hormon* (to excite). It was coined to describe an odorous substance, or substances which initiate a response in another member of the same species. The response may be an immediate one in the form of a change in behaviour, in which case reference to a *releaser pheromone* is made, or it may produce an endocrine or biochemical reaction after a longer period of time—a *primer pheromone*. Originally, the existence of specific substances which release unconditional characteristic responses was suggested. This may be true with insects whose behaviour is stereotyped, but in the case of higher animals with much more complex patterns of behaviour and individual differences, the pheromone concept should be used carefully and only on the understanding that it refers merely to olfactory communication between members of the same species.

The odour-sensitive organs in insects are located on the antennae. Thus in the silkworm moth, *Bombyx mori*, each of the two feathery antennae possesses 10,000 sensory hairs (sensilli). Each sensillium is innervated by one or two receptor cells connected to centres in the brain. Only a single molecule of the odour is required to activate a receptor cell, and the activation of two hundred of these cells initiates a motor response.

The honey bee with its ten different types of glands is a particularly good example of adaptation for chemical communication. The mandibular glands in workers produce a secretion which acts as an alarm signal. In the queen, however, the same gland emits a 'queen substance' containing ketodecenoic acid which transmits different messages depending on the recipient. Thus when digested by workers, this substance prevents them from egg-laying and stops them from rearing the larvae in a way which would produce new queens. On the nuptial flight, the same gland produces a vaporous sex attractant which attracts the drone and induces him to copulate with the queen.

The gypsy moth, *Porthetria dispar*, was the first species whose own sex attractant was exploited for its destruction. Indigenous to Europe and introduced to the USA, it escaped from captivity and multiplied to the extent that it soon infested the whole of New England. The caterpillar of the gypsy moth feeds ravenously on tree leaves causing millions of dollars worth of damage. The flightless female has to attract males in order to mate. She does it very efficiently, emanating an odour which can lure a male from almost one kilometre away. It took a group of chemists thirty years to identify the gypsy-moth sex attractant. They used 500,000 female abdomens to obtain 20mg of the pure attractive substance; it can now be synthesised and is called 'gyplure'.

Thanks to the use of 'gyplure', the gypsy moth has

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THEY FOLLOW THEIR NOSES

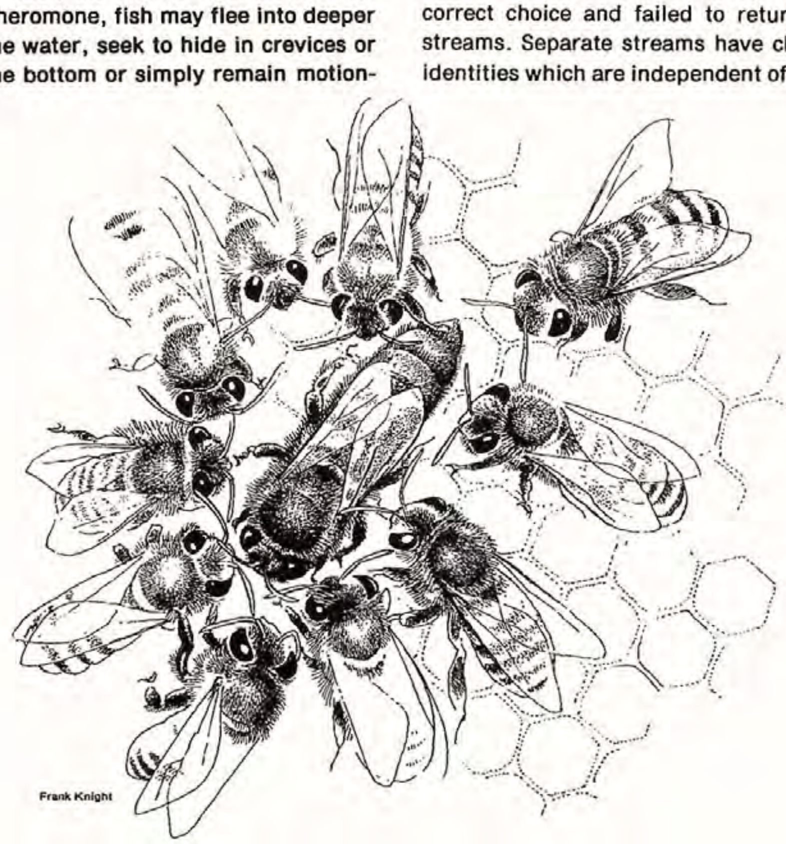
BY R. MYKYTOWYCZ

been prevented from spreading outside the northeast corner of the USA. Traps are baited with the artificial sex lures and insecticides are then applied to infested areas. This monitoring system based on a chemical attractant is used with considerable economic benefit by fruit-growers to prevent fruit-fly infestations of orchards.

However, even in insects reproduction and mate selection is not the only field in which pheromones are involved. A vast number of studies reveal the involvement of odorous substances in such behavioural situations as the selection of food and host, aggregation, defence, territorial marking, maintenance of social order and alarm-raising.

In vertebrates, the best example of the existence of alarm pheromones is provided by fish. Some species possess special club cells in the epidermis which release the alarm substance when the skin is injured. In their reaction to the fear pheromone, fish may flee into deeper water, jump out of the water, seek to hide in crevices or in turbid water on the bottom or simply remain motionless for several minutes. It has been reported that the minnow, *Phoxinus laevis*, after expcsure to alarm substances, avoided a feeding area in a lake for several days. The existence of responses to fear substances has been established experimentally under field and laboratory conditions in many groups of animals.

The astonishing ability of Pacific and Atlantic salmon to return to the places of their birth after prolonged absences has been the subject of intensive studies. It has been shown that their sense of smell is involved, at least partly. To demonstrate this in the case of the silver salmon, *Oncorhynchus kisutch*, fish from two separate branches of a spawning stream were captured. Some were deprived of the sense of smell by blocking the nostrils and released downstream together with others in which the sense of smell was left intact. Many individuals which could not smell, were unable to make the correct choice and failed to return to their respective streams. Separate streams have characteristic chemical identities which are independent of seasonal changes.



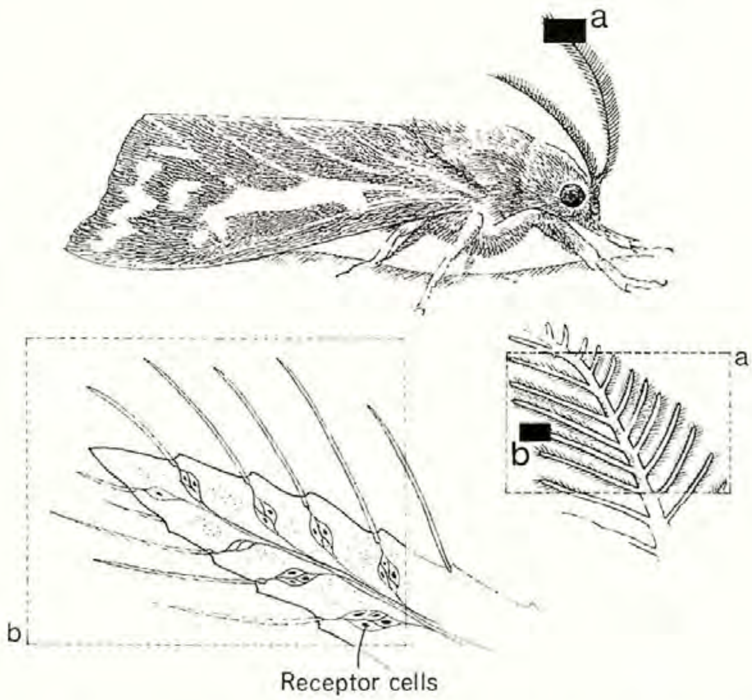
The honey-bee is particularly well equipped for chemical communication. The queen emits odourous substances which affect the behaviour of workers and drones.

In the perception of odours, the key role is played by the olfactory epithelium which in mammals, including man, lies at the centre top of the inside of the nose close to the cribriform plate of the ethmoid bone. Placing an electrode in contact with the surface of the olfactory epithelium or in the olfactory bulb which is another part of the olfactory system located at the base of the brain, permits the recording of the electrical reactions to odour stimuli. When the olfactory apparatus is stimulated by a brief puff of air containing particles of odour, there is a rapid physiological reaction, the response then falling off gradually. This basic technique is widely used in olfactory studies. Permanent implanting of electrodes in the olfactory bulb permits the recording of nerve discharges in the free-moving animal in different behavioural situations.

Animals may also obtain additional information on the properties of various odours through the free endings of

reproductive state of a female even before any external signs of oestrus are visible. Sniffing urine is very common in many mammals particularly ungulates or hoofed mammals such as goats. The sniffing of urine is associated with a characteristic form of grimacing termed, from German, 'Flehmen'. In a typical 'flehmen', an ungulate mammal stands open-mouthed with the head extended and elevated while the upper lip is retracted, wrinkling the nose and baring the gum. In some species including cats, rapid licking movements and mouthing may accompany or follow 'flehmen'. All animals known to display 'flehmen' have a well developed vomeronasal organ and accessory olfactory bulb. Males of some species, notably the billy-goat, not only sniff at urine but draw it into their nasal cavity.

It is, however, in snakes that the function of the vomeronasal organ is most important and most clearly understood. In snakes and lizards this organ is com-



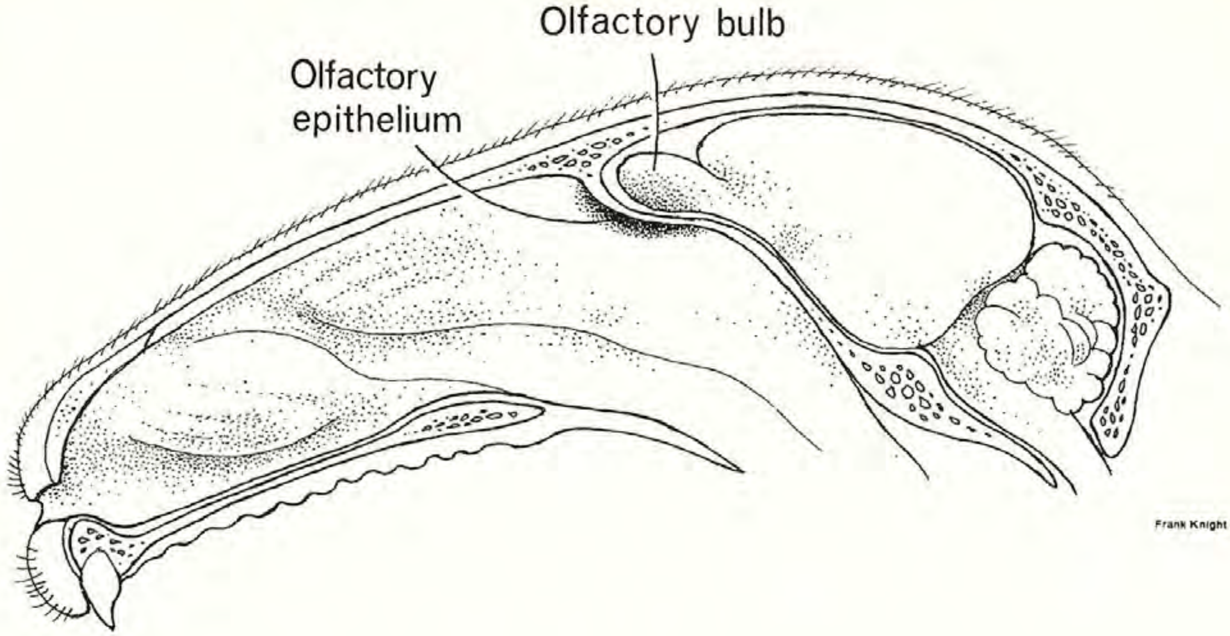
Odour sensitive organs of the moth are located on the antennae. The nlarged segment of the antenna shows the receptor cells vhich are connected to centres in the brain.

the trigeminal nerve in the nasal mucosa. In some species, the sensitivity of this system to certain odorants may be even higher than that of the main olfactory apparatus. The trigeminal nerve is extremely well developed in the platypus.

Most mammals possess still another olfactory system, namely the vomeronasal, or Jacobson's organ, which is located in the nasal cavity on both sides of the septum. It opens either anteriorly into the nasal cavity or by way of the nasopalatine canal into the mouth cavity, and has a sensory epithelium similar to that of the main olfactory system and is connected by the vomeronasal nerve with the accessory olfactory bulb. Observations to date suggest that the Jacobson's organ functions as a special chemo-receptor for sex hormones and their breakdown products secreted in urine.

Smelling of urine permits a male to detect the

pletely separated from the nasal cavity. In the past there has been a lot of speculation on the function of the characteristic tongue-flicking of snakes and lizards. Aristotle noted this behaviour and suggested that the snake's tongue is forked into two tips with fine hair-like ends because of their liking for dainty food. He suggested that by this device, the snakes derive a twofold pleasure, their gustatory sensation being as it were, doubled. Many other fanciful interpretations were made. Now, however, we know for sure that in snakes and lizards, the tongue is part of the smelling mechanism. The flicking tongue picks up odorous particles from the air and transports them through the openings in the palate to the Jacobson's organ. In some species of snakes there is a gap in the lips at the front of the mouth so that the tongue can be flicked out continuously without opening the mouth. Cutting off just the tips of the tongue

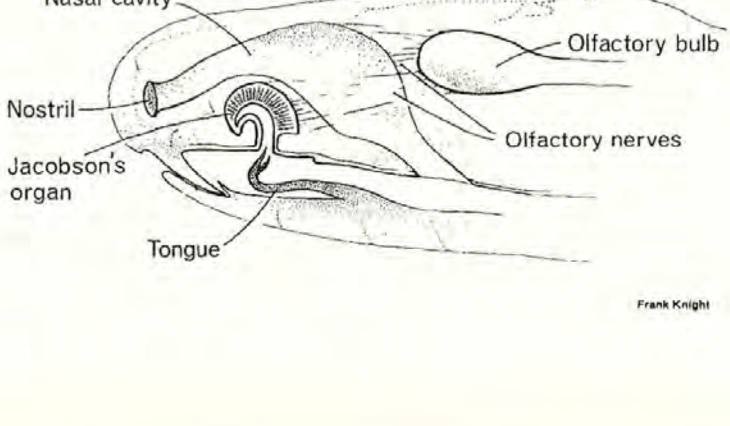


Sagittal section of a rabbit's head showing the location of olfactory epithelium and olfactory bulb.

impairs a snake's ability to detect food. In the European grass snake, *Netrix netrix*, this sort of manipulation practically eliminates the ability to track prey. Well acclimatized captive rattle-snakes, *Crotalus* spp., do not rely upon Jacobson's organ to detect prey and to direct their predatory attack. They use this sensory system, however, to locate escaping prey after striking. Rodents which have been bitten by a snake may wander several metres before dying.

Olfaction is also involved in the reproductive activities of snakes. It has been shown that female garter snakes, *Thamnophis sirtalis sirtalis*, produce oestrogen-dependent olfactory cues which allow males to distinguish between receptive and non-receptive individuals.

The role of the odour of urine in reproduction has been particularly intensively studied under laboratory conditions in mice and rats. Three phenomena have been reported. First, when female mice are kept together in one group their reproductive cycles become disrupted. On the other hand, Dr. Wes Whitten, when experimenting with mice at the Australian National University, noticed that the presence of a male mouse or its urine induces oestrus in groups of females. A high proportion of pregnancies fail, however, if female mice are housed with, or near strange males or become exposed to the smell of urine from alien males. Rendering females unable to smell prevents the above-mentioned phenomena from occurring. Application of male urine to



Most mammals and reptiles possess a Jacobson's organ, lined with olfactory epithelium. While flicking its tongue, the snake picks up odour particles from the air and transports them to this organ through the openings in the palate.

the nostrils of young females for a few days accelerated the onset of puberty while the application of female urine delayed this process. The substance responsible for the male-induced changes is associated with the protein fraction in the urine.

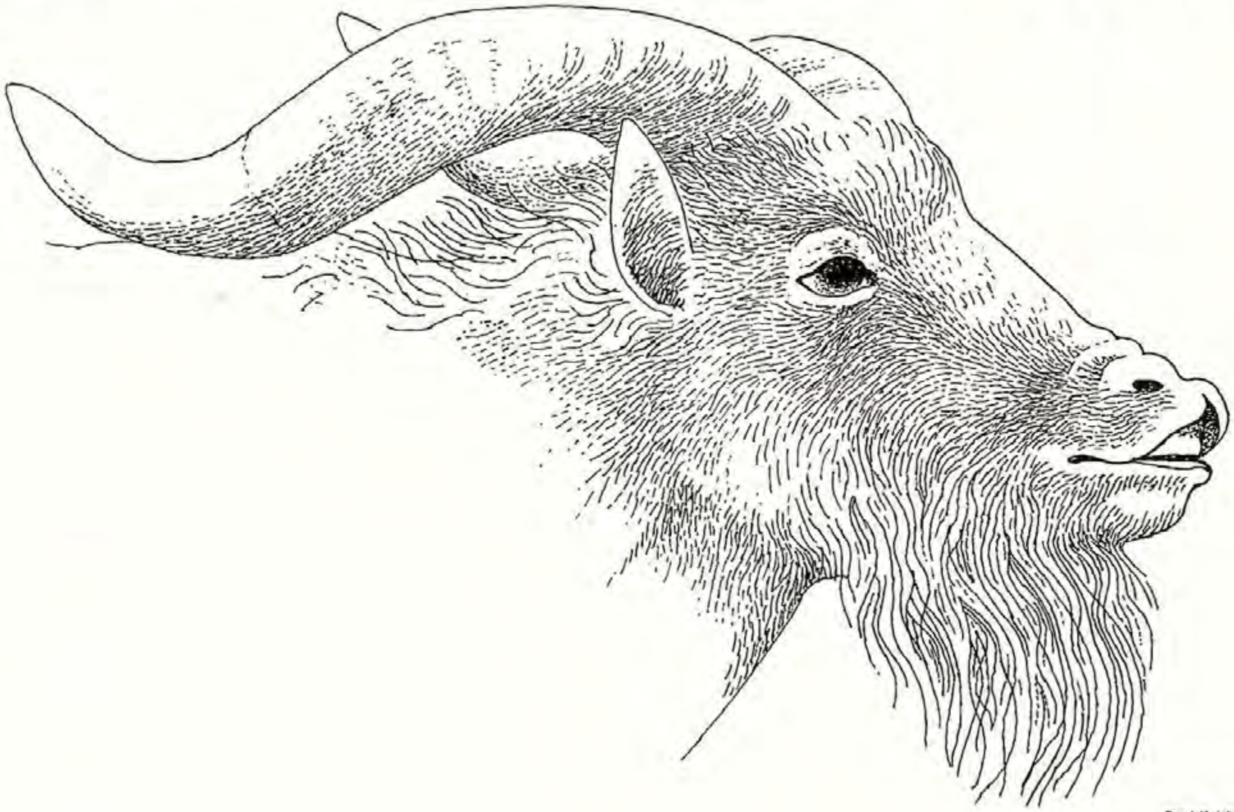
To illustrate the behavioural role of the odour of saliva it is best to refer to the domestic pig. When a boar meets a sow in oestrus, they most frequently adopt a head-to-head posture. Another characteristic of such an encounter is that boars champ their jaws and salivate profusely. In response to the smell of the male's saliva, the female adopts the mating stance. The behaviourally active component of the boar's saliva is a steroid with a urine-like smell. Exposure of a male to an oestrous sow stimulates a rapid rise in the level of this salivary steroid in the blood. Although produced in the testicles, it is transported by the blood to the salivary glands which seem to act as a reservoir. This steroid is responsible for an unpleasant taint which lowers the commerical value of boar's meat. The submaxillary glands in the mouth are larger in male pigs than in females. Boars from which the submaxillary glands have been removed surgically are less able to elicit the mating cooperation in sows and often become the subject of female aggression. It is interesting that the same steroid is present also in human sweat, but its behavioural function is not yet known.

The pig's salivary steroid, the first mammalian pheromone to be synthesised, is now put to practical use during artificial insemination. An aerosol containing it is employed to detect the presence of oestrus in sows which do not display visible symptoms. When blown into the face of an oestrous female it initiates the typical 'leg-locking' mating stance.

Like many other gregarious animals, pigs display a strong group organization. This form of behaviour, although useful under natural conditions, is undesirable under domestication. When the penning of mixed groups of weaners is attempted, serious aggression occurs. The condition of pigs can also be seriously affected by fighting during transportation or grading. Cannibalism, tail and ear-biting and the rejection of sucklings put with a foster mother often take place. Odour is effectively used now to eliminate these undesirable forms of behaviour. A veterinary company in Australia has developed an odorant aerosol which when sprayed over pigs in a pen, masks all pre-existing odours and promotes mutual tolerance. In this context, one cannot resist drawing an analogy with our own behaviour, mainly the rejection of others on account of their odour, be it personal, the food they consume or even the perfume they use. The importance of odour in the formation of social groups or in species recognition has been confirmed by experiments in which animals including guinea pigs and rats have learned to accept artificial scent such as xylol or the odour of violets as their own.

The most important sources of odour in mammals are the specialised, odour-producing, skin glands, which are present in all species. Their location on the body and the ways in which their secretions are used vary. Among Australian native mammals, the brush-tailed possum, *Trichosurus vulpecula* possesses a scent gland in the sternal or chest region. Rubbing of the sternal glands against various objects has been observed to take place under conditions which suggest that their function is to warn off conspecifics, particularly of the same sex.

Flehmen is a characteristic form of grimacing associated with the testing of urine. It is exhibited by many ungulates including the goat. The smelling of urine permits a male to detect the reproductive state of a female.



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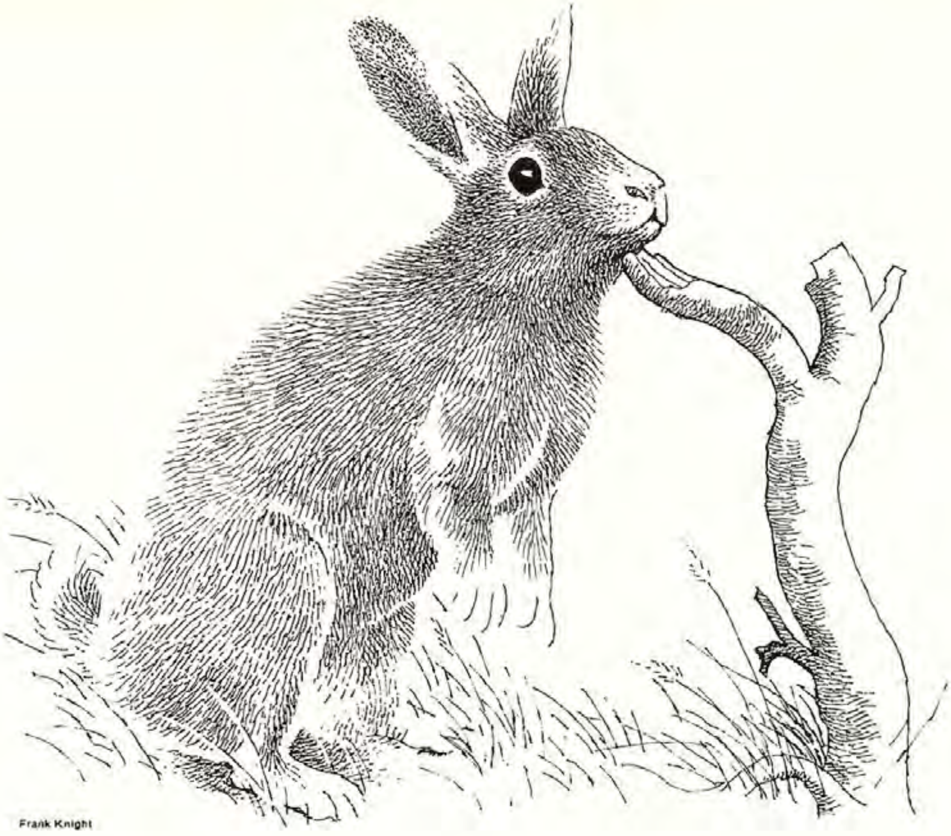


A rabbit applying secretion to a tree stump from the gland situated under its chin.

Similar glands occur in larger species of marsupials such as the grey kangaroo, *Macropus giganteus* and the red kangaroo, *Macropus rufus*. During sexual excitement or aggression, mature male kangaroos rub their chests on a post, on a bush or along the ground.

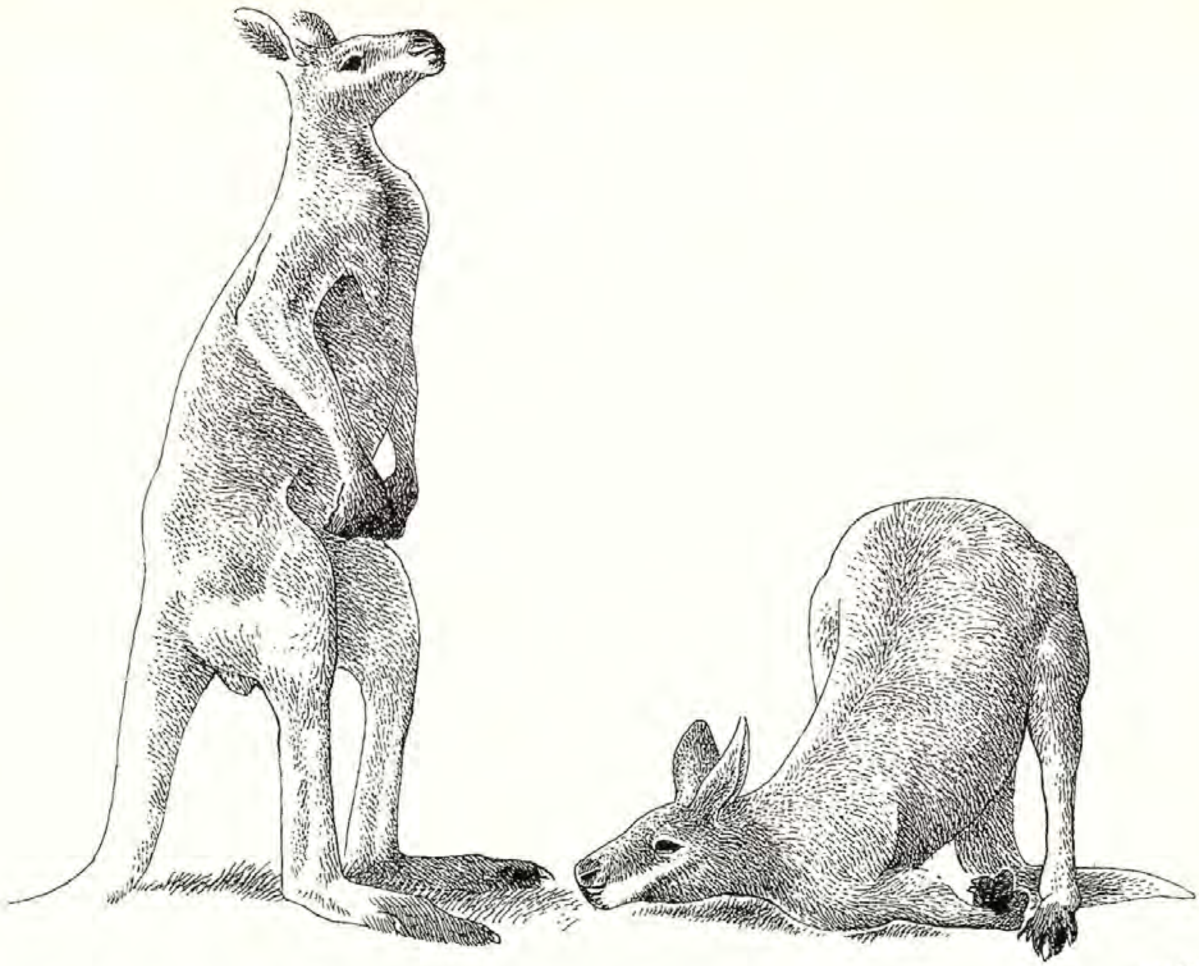
The sugar glider, *Petaurus breviceps papuanus*, is particularly well equipped with odour-producing glands. One on the forehead, produces a yellowish-brown secretion with a strong musky odour which is used to mark other members of the same group. In addition there are glands on the males' feet, chest and in the anal region. There is experimental evidence that the saliva of the sugar glider is also odorous.

Dr. John Nelson of Monash University who spent considerable time studying the ecology of the flying-fox, *Pteropus polycephalus*, reported on the importance of the secretion from the glands in their shoulders, in the formation of groups.

Experimentation with many species of mammals, including the brush-tailed possum, has established firmly that skin glands are controlled by sex hormones—particularly androgens. The injection of testosterone propionate into immature male brush-tailed possums induced rapid development of the sternal gland whilst castration of the sexually mature caused its regression. Injection of male hormone also stimulates the development of the sternal gland in females. The size, secretory activity and the behavioural use of the skin glands fluctuate seasonally in response to changing levels of sex hormones.

There is also a very strong correlation between odour-producing glands and the behavioural status of an animal. Indeed in some animals, and in particular the European wild rabbit, *Oryctolagus cuniculus*, it is possible to determine the dominance ranking of individuals by comparing the degree of development of their odoriferous glands. Thus the ability of an animal to disseminate its own odour or, in other words, to communicate with conspecifics, decides its social rank. Although the secretions from skin glands are used to communicate a wide range of messages, attention has usually been paid to their role in the marking of territories. The wild rabbit possesses an especially strong urge to protect its own territory. The space which an individual or a group occupies is an important factor in determining survival and breeding success. As overcrowding is undesirable, strangers have to be excluded, if necessary by force. The rabbit can fight very viciously, but the use of aggression is minimised under natural conditions because of olfactory marking of a territory by its occupants. The odour used by rabbits for territorial marking is derived from two sources, the anal gland and the chin gland (see *Australian Natural History* 1964, pp. 326-329). These odour-producing glands are larger in males than females.

Practically all mammals possess anal glands. In some, such as the domestic dog, they attain a considerable size. The anal gland in the rabbit is situated around the end portion of the rectum; as faecal pellets are voided, they become coated with the secretion of the anal gland.



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The most important sources of odour in mammals are specialised odour producing skin glands. A male red kangaroo, *Megaleia rufa*, possesses such glands on the chest and one is shown here depositing its secretion on the ground.

Rabbits, particularly males, which are mainly concerned with territorial marking, deposit their faecal pellets on strategically selected sites known as buck- or dung-hills, and thereby warn off intruders.

Although in many instances animals distribute their own odour unintentionally, purposeful distribution is very common. It is often associated with seemingly unnatural, grotesque posturing. Thus the characteristic 'chinning' action of rabbits involves deposition of secretion from the chin gland. In the course of 'chinning', their own odour can be deposited precisely onto various objects. Many mustelids such as weasels, adopt a handstand when applying the secretion from their anal glands onto elevated objects. The spiny anteater, *Echidna aculeata* and guinea pig, drag their hind quarters along the ground during the application of the anal gland secretion. The skunk, *Memphis memphis*, in a defensive action, can eject the secretion from its anal gland with great accuracy over a distance of 4-5 metres. Other species including the rabbit can eject urine some distance with a similar degree of efficiency.

The spraying of a partner with urine is an integral part of the rabbit's courtship as well as aggressive behaviour. Also, self enurination is practised by some species, particularly during the breeding season. Billy-goats are especially proficient in this, directing urine onto their abdomens, briskets and beards. Other ungulates, instead of applying the urine directly to their bodies excrete it onto wallowing places. After selecting a patch of ground they stamp, paw and urinate on it. A muddy excavation results, in which the male rolls himself repeatedly. Females seek and fight for access to a wallowing place maintained by an attractive male.

The deposition of an animal's own odour functions not only for repelling of competitive intruders but even more importantly, for strengthening the individual's familiarity and self-confidence within the occupied space. In a large series of experiments, pairs of wild rabbits unknown to one another were introduced together into a neutral testing area. The odour of one of them, or the odour derived from its cage mate was also introduced into the pen. In the tests using anal- and chin-gland secretions, up to eighty percent of the rabbits familiar with the introduced odour emerged as dominant. The odour from the inguinal (groin) glands which function for individual identification did not produce the same result.

Evidence has been accumulating recently to suggest that, contrary to general assumption, at least some species of birds have a well developed sense of smell and rely on it in their everyday life. Birds are equipped with central and peripheral olfactory apparatus which is anatomically similar to that in reptiles and mammals. Comparisons of the size of the olfactory bulb suggest that in such birds as the vulture, kiwi and tube-nosed marine birds, olfaction could be of primary importance and that most water birds, marsh dwellers and waders may also have a useful olfactory sense. In fact, these speculations have been substantiated in some cases by behavioural observations.

Of all the avian species, the kiwi, *Apteryx australis*, possesses the largest olfactory bulb. This flightless, almost sightless, nocturnal bird, sniffs noticeably. It has been shown experimentally to be able to detect food buried under the ground and screened by nylon mesh.

With regard to the tube-nosed marine birds, their keen sense of smell has been exploited for years by the people who collected them for museums. Collectors take to the open sea in a boat and slowly traverse a certain area, pouring melted fat onto the water. Although originally no birds may be in sight, on returning along the same route, petrels can be seen and collected. More recently, the dependence of petrels and shearwaters on smell during feeding and migration to the nesting burrows has been investigated. Leach's petrel, *Oceanodroma leucorrhoa*, taken from burrows and released the same night, did not return for a week if their nostrils were plugged or olfactory nerves were transected. They returned immediately, however, if left intact. Captive breeding petrels when given a choice always selected the odour of their own nesting material in preference to material collected from a forest-floor.

In their homing, pigeons, *Columba livia*, rely not only on visual marks but also on naturally occurring airborne odours. When deprived of olfactory perception, they either completely lose the ability to home, or return to the aviary much later than control birds.

In a well-controlled field study in California, evidence has been collected to suggest that the turkey-vulture, *Cathartes aura*, depends on olfaction to locate its food. Among other substances, mercaptan, occurring in carcasses and natural gas was used to demonstrate their ability to detect smell. When the results were published, engineers employed by a gas company claimed that they were always aware of this phenomena because when a leakage occurred in the gas pipeline, they watched for the position of circling vultures to locate the exact spot requiring attention.

But what of the role of odour in our own life? It seems that it is not so much our inability to smell, but rather the lack of mental preparedness to use the nose that is responsible for our lesser dependence on it. In fact, experimental proof is available that in some instances man's olfactory acuity is not much different from that of a dog.

Man is not only able to detect scents but like other mammals, is well equipped with several types of skin glands which are the sources of his odour. Thus, apart from the glands situated in the armpits, we possess odour producing glands on the soles of the feet, in the preputial sac and vagina, in the pubic region, in the circumoral areas in the eyelids, in the external auditory canal and around the nipples. The largest of the skin glands, the mammary gland is itself odoriferous. Each of these organs produces a different, characteristic odour.

Investigations into the role of olfaction in animals' lives, particularly in reproduction, has renewed interest in our own sense of smell. The perfume industry was first to recognize the importance of this method of communication. Some progress has already been made and there are signs that soon we may be able to understand better the value of the oldest (from the point of view of evolution) sense and the persuasiveness of our silent language.

FURTHER READING

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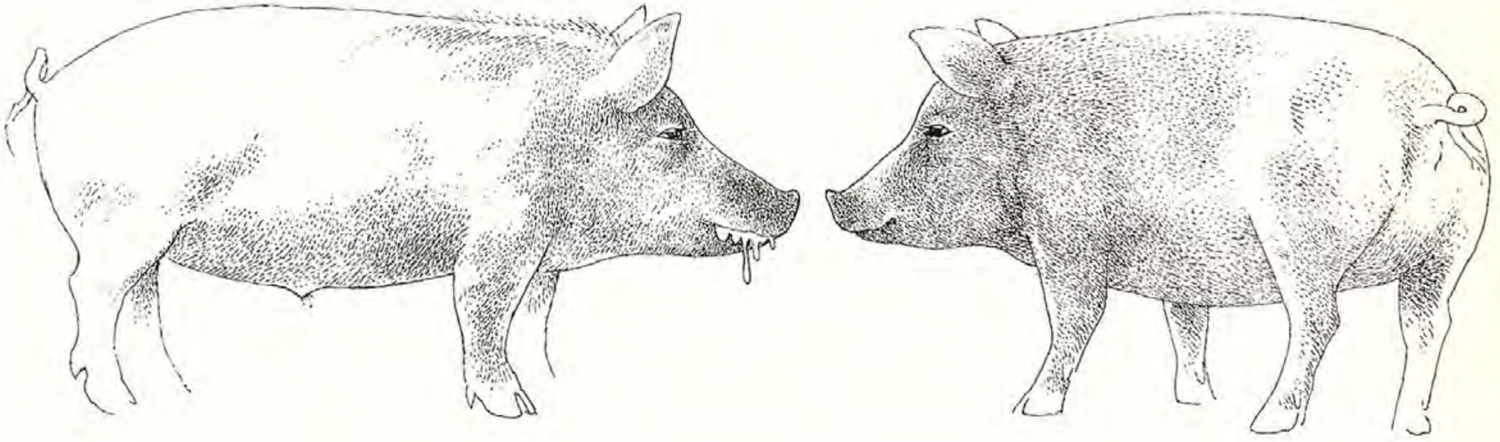
The saliva of a boar contains an odourous steroid which stimulates an oestrous sow to adopt the mating stance.



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A TASMANIAN TRIASSIC STREAM COMMUNITY

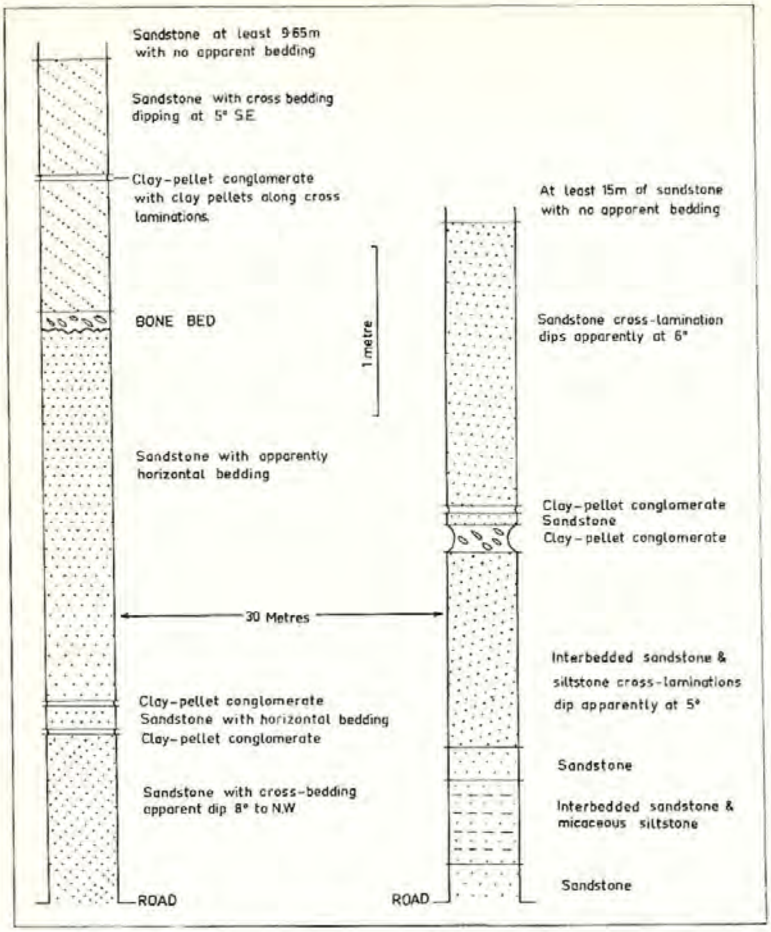
BY MAXWELL R. BANKS, JOHN W. COSGRIFF AND NOEL R. KEMP

One of the lesser known results of the collision of the ore-carrier *Lake Illawarra* with the Tasman Bridge in January, 1975, was the recovery of about fifty tonnes of bone-bearing rock from a known fossil site near Old Beach on the east bank of the Derwent River north of Hobart. The removal of the Tasman Bridge as the traffic link between Hobart and the eastern shore of the Derwent River resulted in the need for widening and upgrading existing roads along the eastern shore between the Bridge and the first bridge upstream, at Bridgewater. The Old Beach Road, previously a picturesque but narrow and winding road, was one of the roads widened. Widening of the road at the fossil site allowed the recovery of large amounts of rock containing the skeletal remains of fish, amphibians and reptiles from the fossil site located directly opposite Dogshear Point.

MAXWELL BANKS is Reader in Geology at the University of Tasmania. He is interested in Tasmanian Stratigraphy and fossils. JOHN COSGRIFF is Professor of Biology at Wayne State University, Detroit, Michigan, USA. He is a Vertebrate Palaeontologist and is especially interested in Triassic Amphibians. NOEL KEMP is Curator of Geology at the Tasmanian Museum, Hobart. He is interested in Vertebrate Palaeontology, and has a particular interest in tertiary sharks' teeth and Triassic Reptiles.

A reconstruction of the early Triassic landscape at Old Beach.

Painting: Jennifer Rofe from J. Cosgriff



Banks, Cosgriff and Kemp

Detailed stratigraphical sections at and near the Old Beach fossil site, measured by Noel Kemp.

The fossil site is a conglomerate lens within the Knocklofty Formation, a sandstone unit of early Triassic age extensively exposed in southeastern Tasmania. The Triassic is the first of three Periods that comprise the Mesozoic Era, or, as it is better known, the 'Age of Dinosaurs'. The vertebrate fossils recovered from the Old Beach site together with similar material collected in the past from other sites within the Knocklofty Formation date from the very earliest parts of the Triassic, about 230 million years ago. The dinosaurs themselves had not evolved at that time but forms ancestral to them called thecodonts were present in Tasmania and in many other parts of the world.

The presence of fossil bones in the Knocklofty Formation has been known for one hundred and twenty years but bones were collected from Old Beach for the first time only fifteen years ago. Prior to the Tasman Bridge disaster, about five tonnes of fossiliferous rock had been collected at Old Beach and yielded several hundred bones or bone fragments. Once the Bridge was removed and as a result of a crash collecting programme involving many people and institutions, several thousand bones or bone fragments were recovered and preliminary identifications made of most of them. In all, the fossiliferous horizon at Old Beach has proved to be one of the richest beds of vertebrate material of this age in the world. Other places in the world have yielded better and more complete individual specimens but here, although the bones are broken and scattered, they can nevertheless be put together like pieces of a jigsaw puzzle and, by comparison with other material, can be identified and reconstructed.

The fossiliferous bed is a layer of clay-pellet conglomerate up to half a metre thick within a sequence of well-sorted, cross-bedded quartz-rich sandstones. The cross-bedding within the sandstone suggests that currents which deposited the sandstone were flowing from the northwesterly quadrant towards the southeast. Exposed in the cliffs by the new road are other beds of clay-pellet conglomerate which are thinner than the main bone bed but, like it, contain bone. The main bone bed extended over a distance of some thirty metres along the road and about seven metres into the former hill slope. The clay-pellet conglomerate contains rounded fragments of clay of many colours up to a maximum of about 300mm in length, many of them of discoidal shape with the broad face of the disc sloping to the northwest. This imbrication of the clay pellets also suggests a stream flowing from the northwest. Some of the clay pellets contain large numbers of minute arthropod fossils belonging to a group referred to as conchostracans. Although plant fragments are themselves rare in the clay-pellet bed, leaf fragments and stems do occur.

Using the rock types, i.e. quartz sandstone and clay-pellet conglomerate, and the vertebrate fossils, it is possible to correlate the conglomerate with other units in southeastern Tasmania. In some of these other units, additional fossils and particularly other fossil vertebrate animals and fossil plants are found. By these means we may reconstruct the community of living things which occupied southeastern Tasmania early in the Triassic.

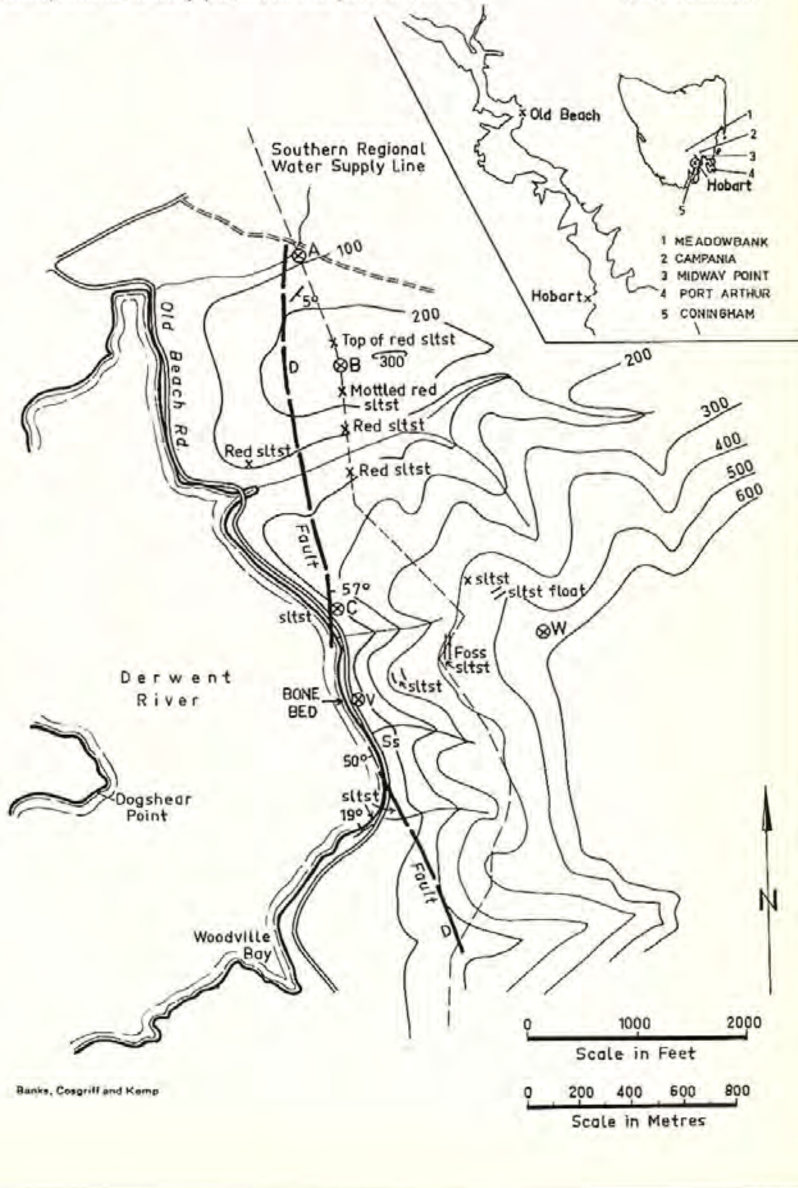
The directions of cross-bedding in early Triassic rocks in Tasmania and the changes in grain size of the quartz grains and of pebbles contained in the sandstones suggest that there were low mountains, well to the northwest. From these mountains, streams flowed onto an extensive flood plain on which there were a few low hills. The plain was composed very largely of sand deposited by meandering rivers as bars within the stream channels themselves or as bars on the banks of the streams. Migration of the meandering streams across the flood plain produced a veneer of sandy material. Here and there were clay pans representing dried lakes and billabongs which filled during floods. While the lakes and ponds persisted, animal and plant life flourished in and around them.

The plant life is shown by fossil leaves and reproductive bodies and spores to include many scouring rushes, low club mosses, some conifers and the maiden-hair trees *(Ginkgo)* and ferns as well as many plants of an extinct group called the seed ferns. In the ponds, minute conchostracans proliferated and may well have been preyed upon by larger crustaceans called malacostracans. Insects were probably present both in the water and in the air above the water. When the lakes and ponds dried up, the animals in them died and their skeletons became scattered about the surface of the clay pan. At times gentle rain fell and the water from surrounding areas drained into the clay pans, covered the skeletons and bones of earlier animals with layers of silt, dissolved some of these bones and re-precipitated the resultant phosphate as nodules lower down in the sediment under the lake floor. At times of higher rainfall, floods swept over the sandy plains, picking up the bones and mudflakes from the dried out lake or billabong floors, washing them downstream. The waning floods left clay balls and pellets as well as bones and bone fragments in the deeper parts of the channel to form a clay-pellet conglomerate. Such was the probable origin of the important bone bed which has now been excavated from Old Beach. The sandstone above and below the clay-pellet conglomerate represents the advancing mid-channel and stream-side sand bars of an early Triassic river. The thin beds of clay-pellet conglomerate of limited lateral extent above and below the main fossiliferous horizon represent minor and probably flash floods. One may envisage a landscape rather like that of some parts of the upper Darling River, New South Wales, or of the channel country of southwestern Queensland but clothed with a different flora and inhabited by a different fauna from the present.

Many of the plants occurring in rocks in southeastern Tasmania which are contemporaneous with the bone bed are plants which show marked adaptive similarities to modern moisture-loving plants. Scouring rushes are abundant as fossils at other places. Modern relatives of these inhabit many of the internal water-ways of Britain, continental Europe and the United States. The bone bed itself contains very rare fragments of club mosses or lycopods and these are found in greater numbers at other sites and at Midway Point branches of lycopod are found in a clay-pellet conglomerate with bones. A particular lycopod, *Pleuromeia*, has recently been a subject of study by G. Retallack, University of New England, who reconstructed it as a low plant forming dense stands in the shallow waters or immediately adjacent thereto. He regarded the lycopods as very largely estuarine or deltaic inhabitants. While this is a possibility for the Old Beach site, the bulk of evidence suggests that this site was rather further upstream. Elsewhere in early Triassic rocks in southeastern Tasmania there are fronds of the fern, *Cladophlebis*, shown in the reconstruction as somewhat akin in habit to a bracken fern. Elsewhere there are sparse remains of seed ferns belonging to the genus *Dicroidium*. When the early Triassic scene was visualised, no reconstruction of these plants by palaeobotanists was available and they were shown as small creeping plants with seeding bodies, and dichotomously branched fronds, inhabiting the relatively moist situations close to the bank of the streams. This reconstruction is based on the close association of *Dicroidium* with the bracken-like fern, *Cladophlebis*, and the lack of fossilised stems which could correspond to the seed fern. It should perhaps be emphasized that no specimens of *Dicroidium* fronds have been found with either reproductive bodies attached (but the cuticle structure of the fronds is virtually identical to that of the reproductive bodies) or of the fronds or reproductive bodies attached to a stem. A South American palaeobotanist, Archangelsky, has suggested that *Dicroidium* fronds belong with a fossil trunk up to one metre in diameter, called *Rhexoxylon*, because of close association of the fronds with the trunks in several places in South America and South Africa. However, this association is unknown in Australia, where *Dicroidium* is very abundant on some horizons.

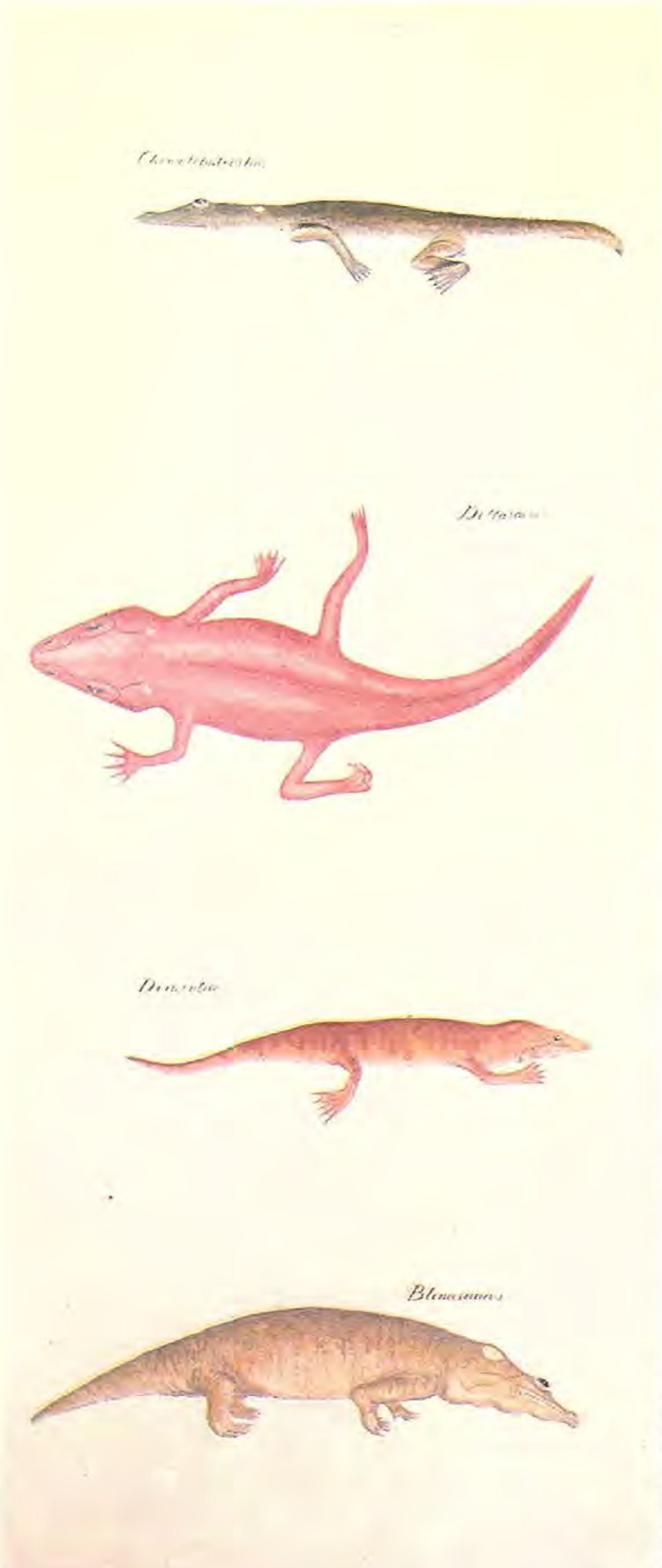
Recently G. Retallack has illustrated *Dicroidium* as a plant somewhat similar to tree or man ferns growing as a heath on poorly-drained lowlands on a flood plain. He has found rhizomes, roots, woody axes and reproductive bodies associated with the leaves of *Dicroidium*, some of which show similar cuticular structure to the leaves. The largest woody axis he found associated with the leaves was 0.1m across and such a size suggests a shrub or low tree rather than a creeper. However, until the various parts assigned to the plant are found in organic contact and the mode and pattern of attachment of the leaves to the woody axis is known, any reconstruction of the plant must be regarded as speculative.

One difficult question concerns the vegetational covering of the sandy plains. Was there one? And if so, what was it? The period with which we are concerned precedes by approximately 150 million years the evolution of grasses and by some 10 million years or so the first evidence of fossil cycad palms in Tasmania. It is possible that the plain was covered by low vegetation of lichens and mosses or of seed ferns which have a more resistent cuticle than the true ferns. However, the very close association in most fossil deposits of *Dicroidium* and *Cladophlebis* suggests that both grew close together and therefore probably in rather wet situations. Perhaps the sandy plain was not covered with vegetation as is true of many inland sandy plains at the present time.



A map of the Old Beach area showing the fossil site. The inset map shows the position of Old Beach relative to Hobart and to the other localities.

Banks, Cosgriff and Kemp



Painting Jennifer Rolfe from J. Cosgriff

Reconstructions of fish, amphibians and reptiles from early Triassic rocks of Tasmania. Colours are hypothetical but were chosen as likely in view of camouflage requirements and by analogy with modern forms.

In the fossil bed itself and in other beds of the same age elsewhere in southern Tasmania there is evidence of some of the invertebrate life of the time. Mention has already been made of the minute conchostracans which flourished in some of the ponds and left their bivalved skeletons in the mud of the pond floor. Some evidence of other sorts of arthropods, the malacostracans and insects, has been detected in contemporary rocks at Knocklofty just outside Hobart and the tracks of shrimp-like crustaceans were found many years ago at Remarkable Cave near Port Arthur in southeastern Tasmania. We may thus suggest that there were water-living invertebrates occupying the streams and ponds of the times.

Fish remains are rather rare in the bone bed as compared with the amphibians which comprise the bulk of the fossil material collected. This is not unexpected because fish skeletons are relatively fragile and would have been readily broken up by the intensity of the floods which carried clay-pellets up to 300mm long. However skull bones, scales, teeth and occasionally large portions of scaled bodies have been collected. *Ceratodus*, the ancestor of the modern lung fish, *Neoceratodus*, is represented by scales and teeth. The teeth are massive, fan-shaped plates that mesh together like the cogs on gear wheels when the jaws were closed; they were adapted to crushing and shearing hard-bodied organisms such as the conchostracans, malacostracans and insects thought to have been present. A tooth row and a number of skull bones indicate the presence of *Saurichthys*, a long-skulled, long-bodied and sharp-toothed fish which elsewhere reached nearly half a metre in length. It resembled the modern garpike of North America in morphology and therefore, like it, was probably an active carnivore. *Acrolepis* is represented by three nearly complete but distorted bodies at Old Beach and by better preserved entire fish elsewhere in the Knocklofty Formation. This genus was a member of the primitive group of bony fish known as palaeoniscids. It was trout-like in body proportions. The small mouth indicates a diet of very small plants or animals or particles of these. *Cleithrolepis*, an interesting but rare fish in the Knocklofty fauna has yet to be identified in the Old Beach matrix. It was a deep-bodied form, growing to about 70 or 80mm in length. A nearly complete body and head was found in a similar stream channel deposit at Coningham so the fish probably lived at Old Beach as well. As in the case of *Acrolepis*, mouth proportions were modest and the diet was therefore composed of small particles.

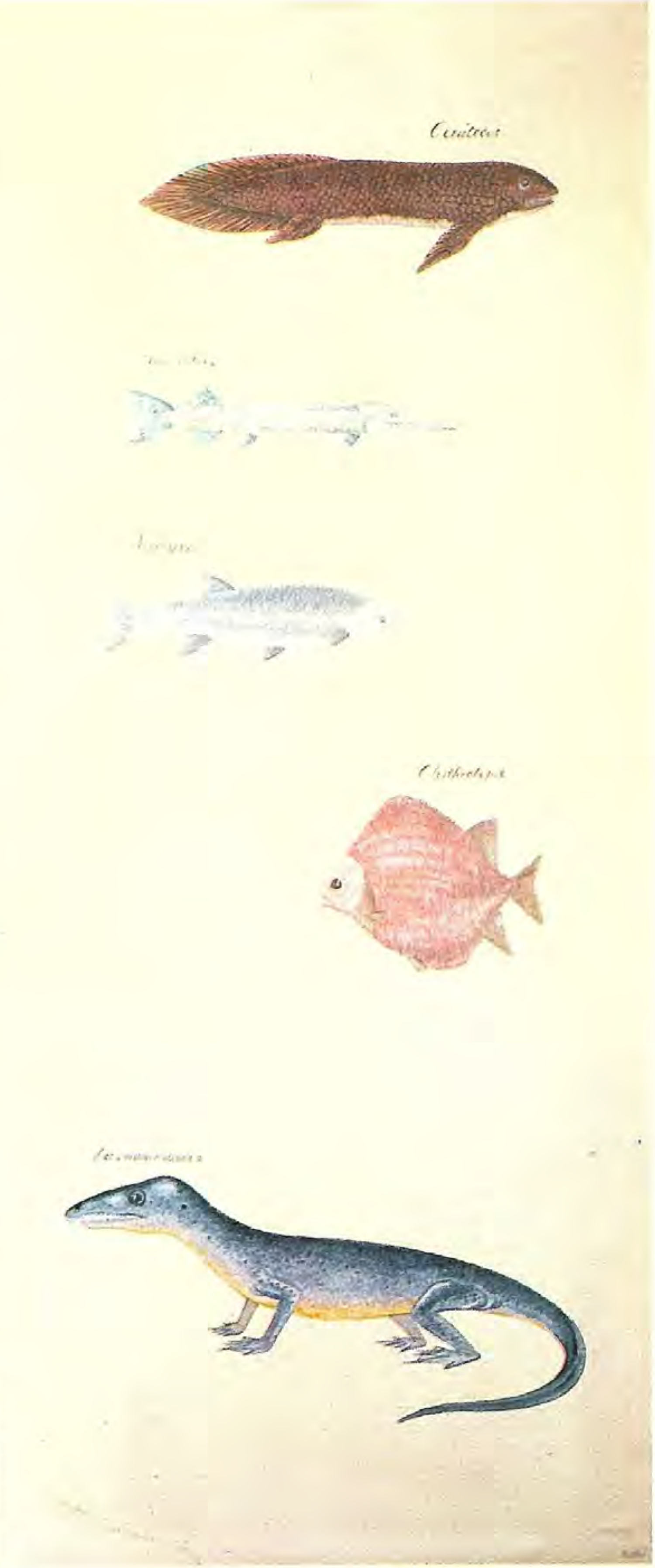
Coprolites, the fossilized dung of extinct vertebrates, are exceedingly common in the Old Beach matrix but it is not possible to associate any of them with particular animals. One broken coprolite about 40mm long contains a bone fragment—memento of an ancient meal.

Reconstructions of the amphibians and detailed examination of the skeletal elements by Cosgriff, together with their relative abundance in the conglomerate and other rock types tell us something of their habits. Morphological features indicating modes of life and types of diet include: extent of the development of the lateral line system (the sensory system employed in detecting vibrations in the water); emplacement of the eye sockets, or orbits, in the skull; the size, shape and number of teeth; and the form of attachment of the jaw muscles. The species represented by the largest amount of bone material were no doubt those living within and on the banks of the stream channels. Those represented by lesser amounts of bone lived in habitats somewhat removed from the channel.

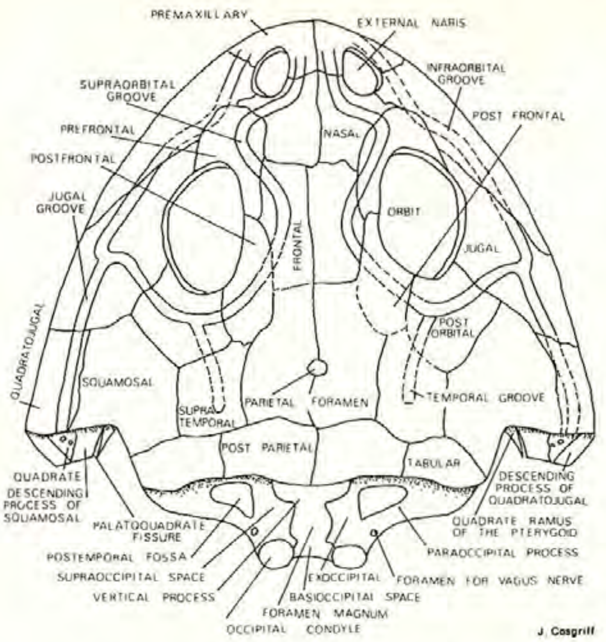
Blinasaurus and *Chomatobatrachus* are by far the most common species in the entire assemblage suggesting that they were native to the stream channel and its immediate surroundings. Each grew to a comparatively large size, up to a metre or more in total length. The bulky, cumbersome construction of *Blinasaurus* and its short, stocky limbs indicate that it was a stream bank or pond bottom dweller rather than an adept swimmer. The position of the eyes on top of the flat skull roof limited the field of vision to upward and lateral directions as would be appropriate to an animal living either under the water or on the stream bank. The powerful jaw musculature and strong sharp teeth signify predation on other large animals. *Blinasaurus* probably divided its time between lurking among the scouring rushes and club mosses along the stream margins and resting immobile on the bottom of quieter stretches of the stream and adjacent ponds. In both settings it would have waited quietly for a potential prey animal to swim by rather than relying on active pursuit to capture it.

Chomatobatrachus was able to move slowly on land but was more adapted to surface swimming, similar to modern crocodiles. In contrast to the other amphibians in the fauna, the lateral line system was very poorly developed and this is strong evidence for stating that it did not engage in much sub-surface swimming. The teeth lining the jaws and over most of the palate surface are comparatively small but very numerous giving the mouth a sand-paper-like lining. The jaw musculature was adapted to produce rapid opening and closing of the mouth—a snapping action—rather than the powerful crushing bite possessed by *Blinasaurus*. All of these considerations—surface swimming, sand-paper dentition and snapping jaws lead to the characterisation of *Chomatobatrachus* as a primarily aquatic form that obtained its food, small vertebrates and/or insects, from the surface of the stream.

Deltasaurus and *Derwentia* are closely related amphibians belonging to the same family. The former reached a considerably larger adult size than the latter. Both are rare elements in the assemblage suggesting that the stream channel environment at Old Beach may have been peripheral to their normal range. This surmise is supported by the fact that one of them, *Deltasaurus*, is the most abundant form in the contemporary Blina Shale of Western Australia. This unit was deposited under lagoonal or deltaic conditions near the strand line, in contrast to the more inland setting of the Old Beach stream. Thereby *Deltasaurus* and *Derwentia* seemed to



Painting: Jennifer Rate from J. Cosgriff



The skull of *Blinasaurus townrowi*, reconstructed by Cosgriff.

have preferred the quiet water regime in areas where flowing water emptied into the sea rather than the more rapidly flowing inland water-ways. Both animals shared with *Chomatobatrachus*, sand-paper dentition and snapping jaws signifying predation on small creatures. In contrast with *Chomatobatrachus*, however, the lateral line system is well-developed meaning that sub-surface swimming was a normal activity. *Deltasaurus* and *Derwentia* probably pursued smaller fish, crustaceans and other invertebrates beneath the surface. They preferred quieter water downstream from the Old Beach site and only occasionally drifted into the areas principally occupied by *Blinasaurus* and *Chomatobatrachus*.

A few pieces of bone of the fossil reptile *Tasmaniosaurus triassicus*, have also been found. The most complete specimen so far known is the one recovered from the quarry at Knocklofty near Hobart in 1960. This reptile was rather lizard-like with a longish slightly curved snout and many sharp backwardly-pointed teeth suggesting a carnivorous diet. Its limb structure suggests that it was capable of relatively rapid movement.

The arthropods, fish, amphibians, and reptiles clearly represent a natural stream-dwelling and stream-margin community as portrayed in the accompanying panoramic reconstruction. Forming the base of the community were the plants. Presumably these were eaten by some of the insects and perhaps by some of the crustaceans and fish. The crustaceans and insects themselves probably formed the major part of the diet of the fish and amphibians such as *Ceratodus*, *Cleithrolepis* and *Chomatobatrachus*. These species may well in turn have been preyed upon by the larger fish and amphibians such as *Saurichthys*, *Deltasaurus* and *Derwentia* which may have also consumed larval or tadpole stages of the other amphibians. The apex species of this community were the amphibian *Blinasaurus* and the reptile *Tasmaniosaurus* which probably preyed on the larger fish such as *Ceratodus* and the other amphibians. *Blinasaurus* as noted earlier seems to have relied on ambush for its meals while the reptile probably employed active pursuit to obtain its prey.

A water-based community such as this would not have survived a lengthy dry season. The presence of red clay pellets and of phosphate nodules suggests that the sediments of the ponds were from time to time exposed for long enough to produce oxidation and for nodules of phosphate to develop in the sub-surface sediments. For the continued existence of the community, rainfall at the time must have been heavy enough to maintain stream flow or at least standing water throughout the year. Similarly, as some members of the community did not hibernate they could not have survived temperatures at or near freezing. These climatic restrictions limit the possibilities for the Tasmanian Triassic climate from cool temperate to sub-tropical conditions, probably the former.

The significance of the fossil animals becomes clear if we look at their contemporary and in some cases modern relatives in Australia and elsewhere. *Ceratodus* forms a link in an almost continuous chain of evolution within Australia of the Dipnoi—a branch of the lobe-finned fishes—from Devonian times (about 380 million years ago) to the present day. *Ceratodus* differs but little from the modern lung fish, *Neoceratodus*, which first appeared in early Cretaceous times about 150 million years ago. *Ceratodus* had been found in sediments of early Triassic age from Europe, Asia, North America, South Africa, Madagascar, and the Spitsbergen Archipelago (Arctic Ocean). *Acrolepis*, *Cleithrolepis* and *Saurichthys* each belong to different extinct groups of primitive bony fish. As we have seen, each of these is similar in morphology to certain modern but unrelated fish which have evolved independently in parallel fashion at later times. Triassic beds from Europe, India, Madagascar, Spitsbergen and Greenland have yielded fossil remains of *Saurichthys*. Forms closely related to *Acrolepis* have been found in the Triassic of South Africa, Madagascar, Spitsbergen and Greenland and *Cleithro-*

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The skull of *Blinasaurus townrowi*, from the Old Beach bone-bed.

D.M. Banks from G. Retallack

A reconstruction of *Dicroidium zuberi*.

lepis has a close relative in the Triassic of South Africa. Both *Saurichthys* and *Cleithrolepis* are common in the Triassic beds of New South Wales.

The Amphibia, the most abundant group in the assemblage in terms of individual bones, all belong to an order, Temnospondyli, which was very successful, diverse and widespread during Triassic times. Almost all of them possessed the flattened bulky heads and bodies and short relatively feeble limbs indicative of aquatic and semi-aquatic modes of life.

The geographical distribution of the Temnospondyli is of particular interest. *Blinasaurus* and *Deltasaurus* are known from early Triassic rocks of Western Australia and *Blinasaurus* also occurs in the early Triassic of New South Wales. Each of the three families to which the four genera, *Blinasaurus*, *Deltasaurus*, *Derwentia* and *Chomatobatrachus* belong enjoyed a wide distribution during the early Triassic. A representative of each of these three families occur together outside of Tasmania only in contemporary rocks of South Africa but they are variously represented in Antarctica, India, Madagascar, the USSR, North America, Greenland and Spitsbergen.

The reptile *Tasmaniosaurus* is of great evolutionary interest in that it belongs to the primitive group—Thecodontia—from which the dinosaurs were derived although no direct lineage can yet be traced. A close relative of *Tasmaniosaurus*, *Proterosuchus*, occurs in the early Triassic rocks of South Africa, India and Southern China.

Remanent magnetism of the early Triassic rocks in New South Wales implies that the site of Hobart was within ten degrees of the South Pole at that time. Other evidence from within the Triassic polar circle such as lack of glacially deposited rocks and the presence of fossil plants indicative of a sub-temperate or temperate climate, linked with the climate inferred from the Old Beach fauna suggests that there was no ice even at the pole during the Triassic Period. The climate, although lacking extremes of cold and dryness, may nevertheless have been quite cool. This is a possible explanation for the absence of large terrestrial reptiles, common in the Triassic elsewhere, from the Tasmanian fauna. One interesting problem which arises if we accept the palaeomagnetic evidence is that of how plants including maiden hair trees grew so close to the poles. At the present time such trees could not grow within ten degrees of the pole because of the long winter night. The presence of abundant vegetation in the early Triassic of Tasmania suggests that a strong seasonality of the polar regions was not present at the time. This in turn leads to the speculation that the axis of rotation of the earth may have been perpendicular to its plane of revolution about the sun rather than set in its present position 66.5 from the plane of the ecliptic.

The distribution of the fossil vertebrates, especially the tetrapods, strongly suggests land links between the different continents during the early Triassic. Although the Temnospondyli were adapted to an aquatic existence, the presence of even narrow ocean barriers would have prevented them from migrating from continent to continent. Even if they could have tolerated the salt water their bulky-bodied, weak-limbed form would not have enabled them to swim any distance. Their distribution then appears to link not only the present day Southern continents but also continents and smaller land masses of the Northern Hemisphere. This is, of course, in keeping with the increasing amount of geophysical evidence pointing to the existence of an ancient southern land mass continuous with the northern land mass.

Thus with the help of the long arm of chance, much hard work by many people and by appeal to the present as the key to the past, we are able to reconstruct a community which lived in and near a stream in Tasmania in early Triassic times some 230 million years ago.

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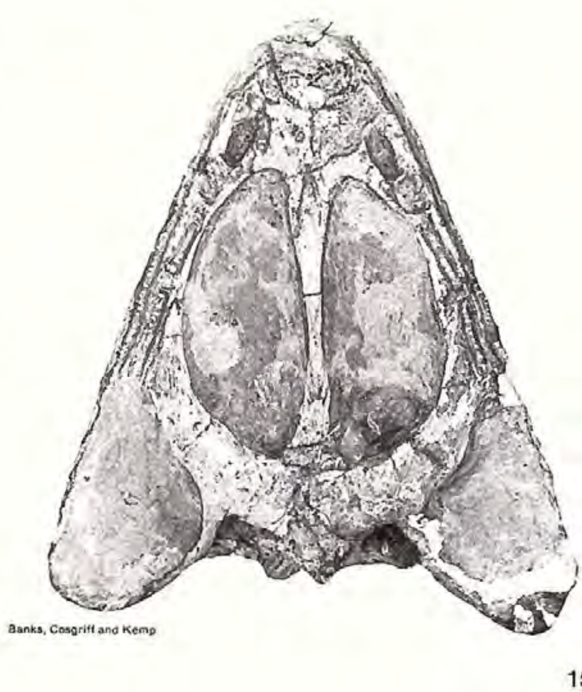

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The palatal surface of *Chomatobatrachus halei*, collected from the Meadowbank Dam site.

BIZARRE OPISTHOBRANCH DEFENCES

BY IAN LOCH

Few groups of animals are more striking than the opisthobranch molluscs or sea slugs, with their bizarre shapes, strange patterns and often brilliant colours. The Opisthobranchia is a subclass of the molluscan class Gastropoda. The other subclasses are the Prosobranchia (marine snails) and Pulmonata (land and freshwater snails and slugs). One of the more obvious differences between the Opisthobranchia and the other two subclasses is the reduction or loss of the gastropod shell, which allows the extravagant expression of body form and ornament. But, in doing so the opisthobranchs sacrifice the greatest function of the molluscan shell, that of defence; and so, some other means of protection has to be found. In doing this, the opisthobranchs show their characteristic diversity and success, using various behavioural, physical, chemical and mechanical adaptations.

In spite of their conspicuous colours and shapes when isolated, very few opisthobranchs are obvious in their natural habitat. The first line of defence is usually obscurity, achieved by blending with a food organism such as a sponge or soft coral which may be as bright as the opisthobranch, or by a shy retiring nature, hiding under rocks, weed or coral, burrowing in sand and being nocturnal. Elaborate sculptural ornamentation including pitting and ridging of the body may be used, as well as general body shape which allows them to merge with the surroundings, like the long slender, flat bodies of those aplysiids which live on seagrasses.

Only a comparative few rely solely on the strength of their chemical defences and adopt striking warning colouration which is obvious in their natural habitat. These animals rely on the 'once bitten, twice shy' principle, so that a predator such as a fish, which will mouth the opisthobranch and violently reject it on finding it distasteful, will in future avoid such colours or patterns. It has been found that when such an opisthobranch is turned on its back, exposing its underside, which is usually of different and paler colours, the fish will readily attack it again, but will stop if the animal rights itself and its warning colours reappear. Because these species are the most obvious, they tend to be collected more often and give an imbalanced picture of their relative numbers. Other species, equally spectacular, may hide during the day and emerge at night, as do the polyps of the hydroids and sea whips on which the opisthobranchs feed and resemble.

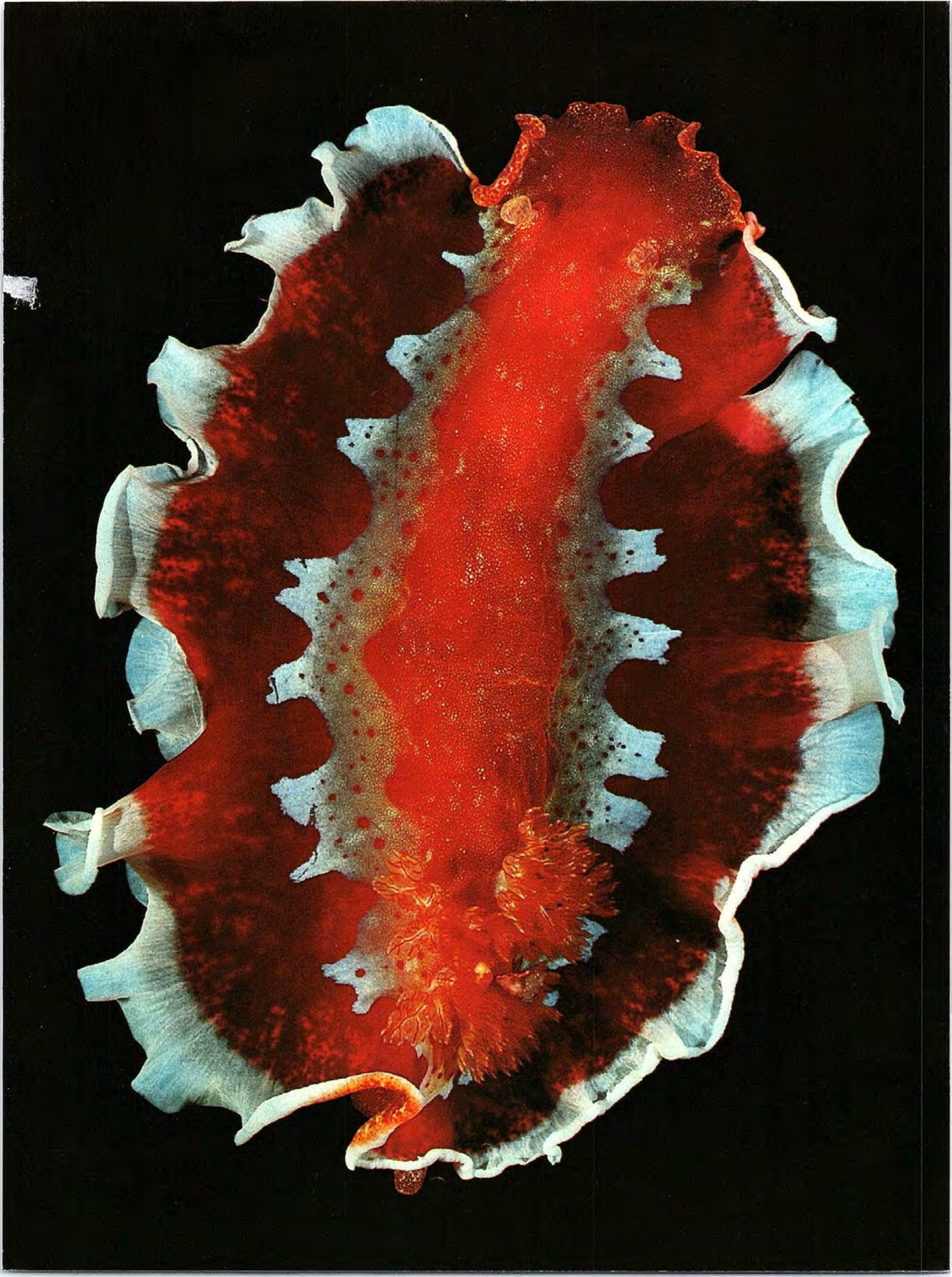
If the first line of defence in cryptic or warning colouration and behaviour fails, the subsequent reactions depend upon the structure of the particular type of opisthobranch. The Opisthobranchia are divided into several orders (see table) according to radula structure, anatomy, etc. Most species, if only lightly disturbed, will attempt to crawl away or hide or burrow in the sand. Delicate sensory apparatus is averted or, if possible—such as in cryptobranch dorid nudibranchs like *Discodoris fragilis*—retracted into the body. Similarly, these dorids can retract the gills or ctenidia, which normally appear as a plumed tuft in their backs, if this is menaced.

TAXONOMY	COMMON NAME	GENERA MENTIONED
Class *Gastropoda*		
A. Subclass *Prosobranchia*	marine snails	*Cypraea, Trivia, Lamellaria, Meb, Murex, Oliva, Mitra, Terebra.*
B. Subclass *Pulmonata*	land and freshwater snails and land slugs	
C. Subclass *Opisthobranchia*	sea slugs	
1. Order Cephalaspidea	bubble shells	*Akera, Philine, Acteon, Bullina, Aglaja.*
2. Order Anaspidea	sea hares	*Aplysia, Bursatella.*
3. Order Notaspidea	side gilled slugs	*Euselenops, Pleurobranchus, Pleurobranchaea.*
4. Order Sacoglossa	sap sucking slugs	*Cyerce, Stiliger, Lobiger, Midorigai.*
5. Order Nudibranchia	naked gilled slugs	*Kaloplocamus, Gymnodoris, Roboastra.*
(a) Suborder Doridoida		*Discodoris, Hexabranchus, Nembrotha, Chromodoris, Dendrodoris, Phyllidia.*
(b) Suborder Arminoida		*Madrella.*
(c) Suborder Dendronotoida		*Melibe, Marionopsis, Hancockia.*
(d) Suborder Aeolidoida		*Myrrhine, Glaucus, Moridilla, Phestilla.*

N Coleman/AMPI

The Spanish dancer, *Hexabranchus flammulatus*, exhibits magnificent displays of colour when swimming or disturbed.

IAN LOCH is a Technical Officer in The Australian Museum's Department of Malacology. He has been collecting and photographing opisthobranchs since 1970.



N. Coleman/AMPI

The Spanish dancer, *Hexabranchus flammulatus*, showing its normal crawling position.

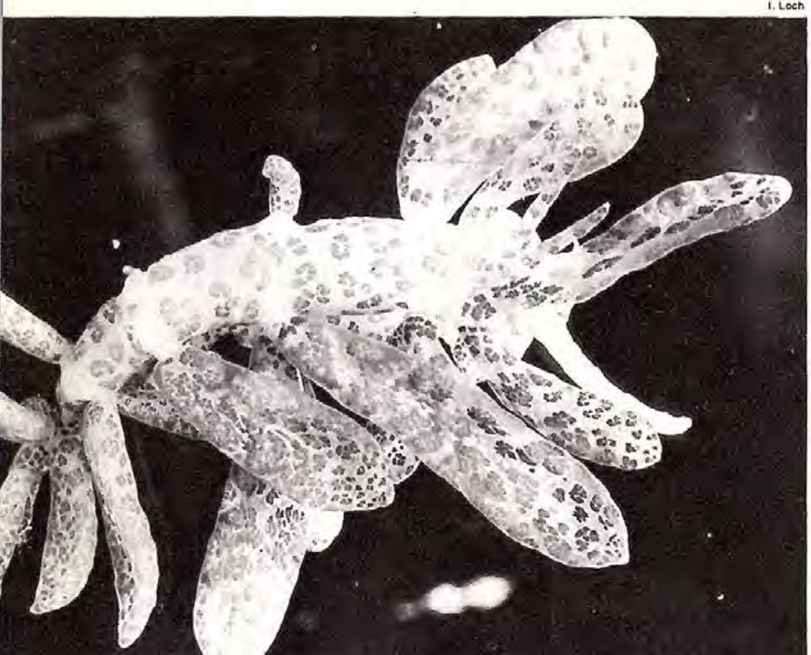
Myrrhine longicitta, closely resembles some soft coral, and when disturbed, casts off its cerata.

Cyerce nigricans, can completely change its appearance when disturbed, by casting off the cerata on its back.

Some species from diverse groups attempt a more active escape and swim away. These include the dorid nudibranch *Hexabranchus flammulatus* and the side-gilled *Euselenops luniceps*, which swim by dorso-ventral flexions of the body. A dorid *Nembrotha* sp. uses violent lateral flexions of its whole body; *Aplysia*, particularly juveniles, use the large parapodia or side flaps, while the cephalaspidean *Akera soluta* uses flaps on its head region, and *Coryphella iodinea*, an aeolid, uses lateral flexions. Generally, swimming is clumsy and only sustained for short periods. It helps little if active predators such as fish are involved, but it can remove the opisthobranch from the reach of crabs and other molluscs.

A few species also swim simply as a means of locomotion, as well as escape. With these, swimming can be sustained for many minutes. They include the dendronotacean *Melibe leonina*, which swims upside down, as does the side-gilled *Pleurobranchus membranaceous*, the aeolid *Coryphella cynara*, which uses its dorsal flaps

I. Loch



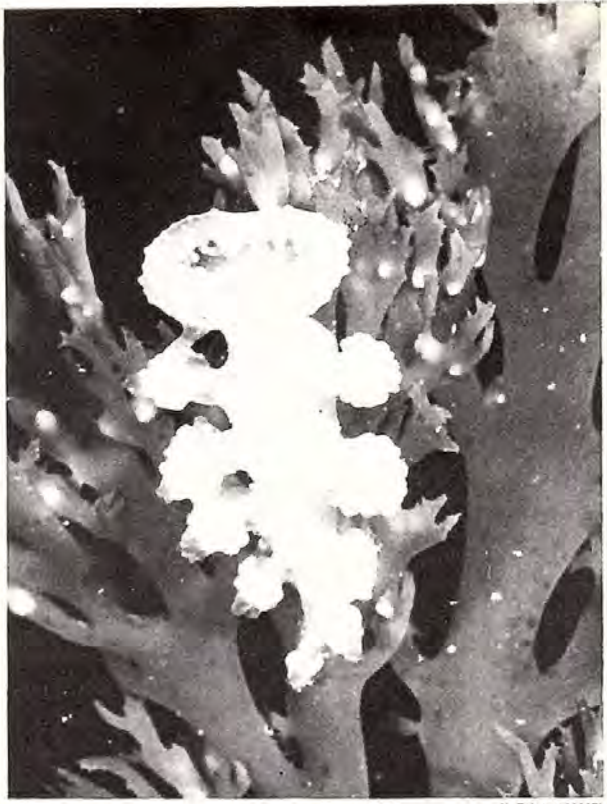
or cerata, and *Hexabranchus flammulatus*, the Spanish dancer. When *H. flammulatus* is swimming, the waves which pass back along the mantle edge expose the brilliant red and white colouration, normally hidden when the animal is crawling as the mantle edge is folded back on itself, and is a russet brown colour underneath. This flashing of bright colours while swimming may be a warning display, but little is known of the chemical defences of *H. flammulatus* except that its skin is non-acidic. One woman has experienced a mild skin reaction after handling the related *Hexabranchus sanguineus*.

Concealment and flight failing, opisthobranchs turn to further measures. Having totally lost the shell, some species, particularly cryptobranch dorid nudibranchs, set about replacing it by having calcium spicules embedded in the dorsal surface of the body to toughen it and make it harder for predators to remove pieces. Rather than invest

N. Coleman/AMPI

resources in solely defensive structures, some rely on adapting old procedures such as mucous secretion, used in a dozen everyday functions such as crawling, digestion and reproduction. Upon attack, copious amounts of mucus are produced, usually at a thicker consistency than normal. This is particularly effective against the jointed appendages of crustaceans such as crabs. *Discodoris fragilis* uses this mechanism, but it has a more dramatic use of existing body structures if harder pressed. As a skink can cast its tail, so this dorid nudibranch can cast off all or sections of its hypernotum, the large, fleshy, laterally projecting margins of the dorsal surface of the animal. This is probably done by water intake into the region of the hypernotum, with muscular constriction along zones of weakness, as the cast pieces are larger than the gaps from which they came. There is no apparent ill effect, but little is known of long-term regeneration.

Other opisthobranchs use autotomy of body fragments on a less extreme scale. With the liberation of the opisthobranch body from the gastropod shell, most orders evolved some forms with elaborate flaps or cerata on the dorsal surface of the body, increasing body surface area for respiration by diffusion etc. Such diverse

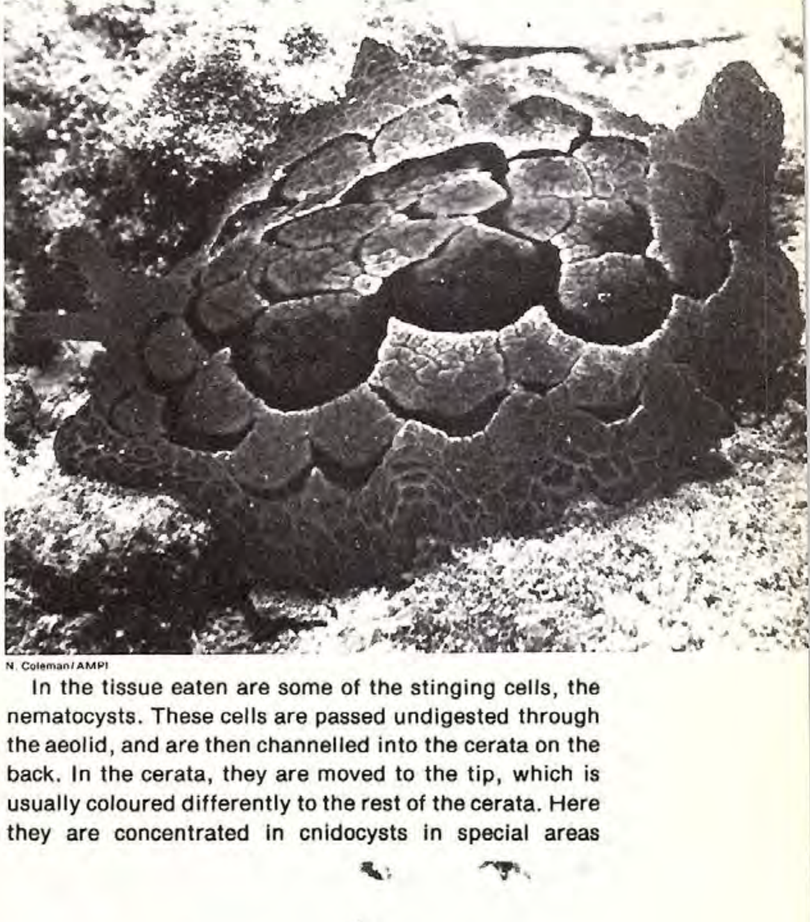


N. Coleman/AMPI

Melibe australis, captures prey with its large, round oral hood.

genera as the sacoglossans, *Cyerce* and *Stiliger*, the sea hare, *Bursatella*, the dendronotoideans, *Melibe* and *Marionopsis*, the dorid *Okenia* and all of the nudibranch suborder Aeolidoida have dorsal extensions from their body. While functioning primarily as gills, these appendages also serve as areas of concentration for other defence mechanisms such as chemical-secreting glands, mucous glands etc., and in the final extreme of defence, can be autotomized and cast off to divert the predator from the more vital head and body. This can be seen with aeolids like *Myrrhine longicirra* and the sacoglossan *Cyerce elegans*, whose cerata are so sticky with defensive mucus that it is very difficult to collect and photograph it without dislodging some or all of them. With some species, like those of *Melibe*, the cast-off cerata continue to move, wriggle and even swim weakly for considerable periods of time, presumably distracting the predator.

Before they reach the extreme of sacrificing parts of the bodies, however, most opisthobranchs use other means of defence. The aeolid nudibranchs have evolved a system of using captured weapons of the coelenterates on which they feed. Almost all aeolids eat coelenterates—hydroids, anemones, corals, jellyfish or their kin—and these coelenterates all use nematocysts for their defence and to kill prey. These nematocysts are tiny stinging cells in the tentacles of the coelenterates, which, when triggered, turn inside out, and the coiled filament inside lashes out so the head penetrates the skin of its victim, introducing toxins. It functions rather like a poisoned dart. The strength of some of these toxins is such that *Chironex*, the tropical box jellyfish, is able to kill people in minutes. Naturally, large numbers of these tiny nematocysts are involved. The aeolids somehow have immunity from their hosts, so that when they crawl on them and feed on them they do not trigger off an attack by the coelenterate. Possibly they can secrete a mucus which the host coelenterate accepts as its own and thus does not recognize them as foreign. (If, however, the aeolid is forced into its host's tentacles, it will be readily eaten.)



N. Coleman/AMPI

Sempers side-gilled slug, *Pleurobranchus semperi*. Most species of the *Pleurobranchus* genus secrete acid when sharply disturbed.

In the tissue eaten are some of the stinging cells, the nematocysts. These cells are passed undigested through the aeolid, and are then channelled into the cerata on the back. In the cerata, they are moved to the tip, which is usually coloured differently to the rest of the cerata. Here they are concentrated in cnidocysts in special areas

R. Kuiter

Pteraeolidia janthina shows wide variations in colour from one individual to another. This species is widely distributed throughout the Indo-Pacific and the colour variations probably reflect changes in diet.

N. Coleman/AMPI

The Aeolid, *Coryphella rubrolineata*, concentrates stinging cells from coelenterates on which they feed, at the tips of their brightly coloured cerata.

called cnidosacs, from which they can be discharged into any predator of the aeolid. As there may be twenty to thirty nematocysts in each cnidocyst and three hundred to four hundred cnidocysts in each cnidosac at the tip of each cerata, of which some aeolid nudibranchs have dozens, the number of these captured nematocysts which an aeolid can have available for its defence can run into hundreds of thousands. Some idea of the effectiveness of this can be gauged from the fact that *Glaucus atlanticus*, a pelagic aeolid which feeds on *Physalia*, the Portuguese man-of-war, has been known, when washed inshore in NSW, to cause swimmers similar but milder stings to those of the *Physalia* itself. Additional behavioural mechanisms are also used to increase effectiveness so that an aeolid such as *Moridilla brocki*, will actively lash out with its cerata to increase the contact with the predator.

The ultimate behavioural variation is that of *Phestilla*, which preys on the polyps of some stony corals. When threatened, this aeolid manages to stimulate the polyps of the coral to defend itself. It does not capture weapons, but simply borrows the whole army. The degree of reliance upon nematocysts varies amongst the aeolids, but nematocysts are also used by a few unrelated opisthobranchs such as the dendronotacean *Hancockia burni*, which feeds on hydroid coelenterates. However, the cerata are used for other defence mechanisms, involving concentrations of glandular tissue for chemical defences. These glands are concentrated on raised bumps or papillae on the dorsal surface of many different opisthobranchs as well as towards the tips of any flaps or appendages.

One of the most successful of the chemical defences is the secretion of acid. The acids used are predominantly sulphuric acid with smaller amounts of hydrochloric acid. The acid is stored in glands in or below the skin. Fish are particularly adverse to acidic food and the use of acid repulses what is potentially the greatest group of predators on opisthobranchs. This chemical defence is used by such diverse groups as the side-gilled *Pleurobranchus*, the dorid nudibranch *Discodoris*, and the primitive bubble shells, *Acteon* and *Philine*. It is also used by some cowries, *Cypraea* and allied cowries *Trivia*, and their relation, *Lamellaria*, which has only a fragile internal shell. These genera belong to a different subclass. *Cycloporus* and *Stylostomum* flatworms from the different phylum Platyhelminthes, also secrete acid upon disturbance. The sulphuric acid produced can be as low as pH1, a very strong acid, particulary for organic production. While acid has a strong deterrent effect, other opisthobranchs with neutral skin pH are also rejected by fish. The presence of further skin glands has been demonstrated, but so far their secretions have been poorly defined. Some of these secretions are visible. The shelled sacoglossans such as *Lobiger*, and the curious bivalved gastropod, *Midorigai australis*, when disturbed produce a milky exudate from the hypobranchial glands which are accessory glands associated with gill cleaning. The shell-less sacoglossans also produce a white defensive fluid from special glands in the body and on surfaces of cerata. A similar white fluid is excreted by the common NSW coastal bubble shell, *Bullina lineata* and by some of the *Chromodoris*, a large group of brightly coloured dorid nudibranchs, if they are roughly handled. It is not known whether all these milky secretions are the same, or what their composition is. Indeed, their defence capabilities are attributed to them simply because they are produced when under stress.

N. Coleman/AMPI

Nembrotha kubargana, secretes a purple dye when it is disturbed. This specimen was photographed in the lagoon at Lizard Island.

Similarly, some but not all of the doridoid *Nembrotha* species will produce a deep purple stain under stress. Again, its composition is unknown as are its affinities with the Tyrrian purple secreted by a wide range of carnivorous prosobranch gastropods such as some *Murex*, *Oliva*, *Mitra*, *Terebra*, etc., and which contains concentrations of the toxic chemical bromine. Tyrrian purple, from some Mediterranean species of *Murex*, was used by Phoenicians to dye cloth and became so expensive that it was eventually used exclusively by Roman emperors as the imperial purple. Most of the members of the Anaspidea, the sea hares, will produce the reddish-purple pigment aplysiopurpurin. The cephalaspidean *Aglaja lineata*, however, will secrete a yellow stain about which nothing is known, apart from the fact it will stain hands. *Madrella sanguinea*, an arminoid nudibranch, with others of its kin, can also discharge pigment cells from the tips of cerata, causing staining. These coloured compounds allow the range of the secretions to be visualised.

Other compounds are colourless and their presence only detected by their effects. Some of these can be imagined when they led an early nineteenth century zoologist to name one species *cespitosus*. Species of *Melibe* have a very sweet musky smell when taken from the sea. Mucus from the large dorid *Dendrodoris* *tuberculosa* produced a burning sensation around the lips and eyes when accidentally transferred there after handling an animal for photography, and mucus from *Dendrodoris gunnamatta* burnt like chili in the mouth. One woman, on cortisone treatment, reacted violently after handling a large shell-less sacoglossan, and needed immediate medical treatment. The dorid nudibranch family Phyllidiidae possesses a toxin which appears unique to their family. A curious group, they have no external appendages vulnerable to attack, and their bodies feel like rubber, but when provoked they produce a poison which, for *Phyllidia varicosa*, has been shown experimentally to be lethal to small crabs, amphipods and fish. Nothing is known about the toxin's chemistry or its mode of action but it has a strong characteristic odour which will persist for prolonged periods in water contaminated by it. A four or five centimetre *Phyllidia varicosa* can contaminate a 100 litre aquarium for hours. Because of their poisonous nature, most *Phyllidia* can adopt bright warning colours and remain exposed on the sponges on which they feed.

An interesting offshoot of this known toxicity is the mimicking of *Phyllidia nobilis* by an undescribed species of the flatworm genus *Pseudoceros*. To succeed as a mimic, an animal must mimic something which is known to be distasteful or dangerous, so that would-be predators will avoid the mimic also. The marine flatworms, which are flat, leaf-like animals, also have no external mechanical protection, but have managed to cope effectively with similar problems to those of the opisthobranchs, often by similar methods. This one species, however, solves its problems by mimicking a *Phyllidia*. It even arches its thin flat body to give a rounded three-dimensional effect like *Phyllidia*, besides having similar colours and patterns. And, as any successful mimic, it is nowhere near as numerous as the common tropical *Phyllidia nobilis* it mimics.

Another phenomenon observed in some irritated opisthobranchs is bioluminescence. The tips of the appendages of a *Kaloplocamus* sp. glow in the dark when it is disturbed. Apart from possibly startling predators, its significance is poorly understood, but it also occurs in related and distant nudibranchs. Other little known areas

Valerie Taylor

Nembrotha sp. now, an undescribed species of Nudibranc from Heron Island, Queensland.

N. Coleman/AMPI

Chromodoris sp., an undescribed species of Nudibranch from the Great Barrier Reef, Queensland.

are the relationship of chemical compounds in opisthobranchs to those in their food organisms. It is probable that they utilize compounds which make their food distasteful to most predators. Certainly, pigments which allow them to blend into red or yellow and other brightly coloured sponges and soft corals appear to be derived directly from their food. However, these compounds are only starting to be looked at in the sponges, etc. Indeed, not only the chemistry is poorly known, but also the very animals themselves, and dozens of species which are new to science occur around Australian coasts.

In spite of their elaborate defences, opisthobranchs still fall victim to a wide range of predators. Some larger ones are eaten by fish, which are probably very hungry or have hard-lined mouths and can ignore the defences. Others may be eaten by flatworms if they are small enough or by shelled molluscs such as the baler *Melo amphora*, which has been recorded eating an aplysiid. Some of the greatest predators are other opisthobranchs, such as the more advanced cephalaspideans *Aglaja* and *Chelidonura*, the side-gilled *Pleurobranchaea*, or the active carnivorous dorids *Gymnodoris* and *Roboastra*.

Generally though, the multi-level systems of defence are more than adequate substitutes for the reduction or complete loss of the gastropod shell, even to the extent that other animals take advantage of their reputation and mimic them. Some species, at least, should be handled with caution.

The assistance of Mr. R. Burn, Research Associate of The Australian Museum, in the preparation of this article is gratefully acknowledged.

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THE QUIDDITY OF TIGER QUOLLS

BY GRAHAM A. SETTLE

GRAHAM SETTLE, Teaching Fellow in the School of Zoology, University of New South Wales, has done extensive studies on parental relations, play and predation in the Dasyuridae: Marsupialia. His primary research interest is sociobiology, especially ethnology and ecology.

G. Settle

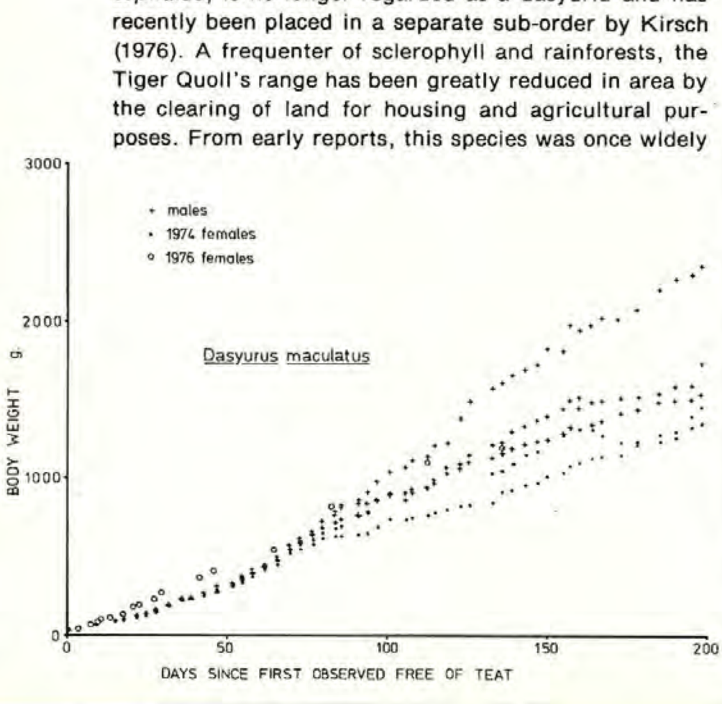
Grumpy and Molly mating. Note the neck grip by the male and the relaxed, eyes closed behaviour of the female.

Possibly the first of the marsupial carnivores to be encountered by white settlers in eastern Australia was a spotted, cat-sized animal which soon established for itself a reputation as a blood-thirsty killer and decimator of the previously well-feathered contents of poultry yards. The vernacular 'Spotted Martin', used by Captain Phillip who first recorded the existence of this marsupial, is by far the most accurate lay term used to describe *Dasyurus maculatus* to date. It is thought this term referred to the peculiar bounding gait of these animals, similar to that of martins and weasels with which the first Governor of the Colony would have been familiar. Unfortunately the term was supplanted with a complete misnomer, 'Tiger Cat', which has remained popular despite its inaccurate connotations. The word 'quoll' is now used to describe those members of the Family Dasyuridae elsewhere referred to as 'native cats' and encompassing the genus *Dasyurus*.

The Tiger Quoll is, then, the largest living member of the Dasyuridae to inhabit the Australian mainland. The only dasyure attaining a larger size is the Tasmanian Devil, *Sarcophilus harrisi*, whose range had contracted to that isle before the arrival of the first non-aboriginal men. The Tasmanian Wolf or Tiger, *Thylacinus cynocephalus*, is no longer regarded as a dasyurid and has recently been placed in a separate sub-order by Kirsch (1976). A frequenter of sclerophyll and rainforests, the Tiger Quoll's range has been greatly reduced in area by the clearing of land for housing and agricultural purposes. From early reports, this species was once widely distributed in all suitable habitats on both sides of the Great Dividing Range from southeastern Queensland, through NSW and Victoria to South Australia and Tasmania. Now, either extremely rare or extinct in South Australia, it is uncommon throughout much of the remaining habitat, though it should be remembered that population numbers of medium-sized predatory mammals are often low in relation to the area they inhabit. It was once well-known around Sydney and is still found in some bushland areas on the southern side of the Hawkesbury River with the exception of rural and urban areas. Small Tiger Quoll populations occur north of the Hawkesbury and it could be regarded as fairly plentiful in the rugged New England escarpment country east of the Great Divide. A sub-species, *D. m. gracilis*, is found in north Queensland to the west of the Cairns region.

The Tiger Quoll is, as are other members of the genus, spotted with numerous white blotches on a background of dark to olive brown. It is, however, easily distinguished from the other quolls by the presence of spots on the tail and five toes, compared with four, on the hindfoot. The under surface is a pale creamy yellow. The sexes differ in both size and colour, the male attaining a weight of up to seven kilograms, while the females only reach four kilograms and are generally darker than the males. The pouch of the female opens anteriorly and contains six teats. The foot pads are ridged and this species is the most arboreal of all the quolls.

The Tiger Quoll was one of the earliest dasyurids to be described but remarkably, has rarely been the subject of scientific study. Two of the animals described in this article, Ray and Ann, together with Ann's five young, Grumpy, Morris, Benny, Molly and Margot were captured in October 1974 in Carrai State Forest, approximately eighty kilometres west of Kempsey, NSW, at an altitude of nine hundred and thirty metres. The terrain is mountainous and characterised by two dominant vegetation types: New England hardwood forest on the ridge tops, and rainforest in the valleys. Extensive selective logging of the forests over many years has resulted in a mosaic of logged areas in various stages of regeneration throughout much of the region. Tiger Quolls could be regarded as common in this area and still cause considerable annoyance to local farmers. Ray and Ann were caught on the same night in two traps only ten feet apart, Ann having the five young in her pouch which she subsequently reared successfully in captivity.



NAMES AND ORIGINS OF ANIMALS USED IN THE STUDY

Name	Sex	Birth Date	Origin
RAY	♂	Unknown	Caught Carrai, 1974
ANN	♀	Unknown	Caught Carrai, 1974
GRUMPY	♂	Approx. 5/9/74	Wild mating (Ray X Ann?)
MORRIS	♂	Approx. 5/9/74	Wild mating (Ray X Ann?)
BENNY	♂	Approx. 5/9/74	Wild mating (Ray X Ann?)
MOLLY	♀	Approx. 5/9/74	Wild mating (Ray X Ann?)
MARGOT	♀	Approx. 5/9/74	Wild mating (Ray X Ann?)
POLLY	♀	20/8/76	Molly X Grumpy
WRIGGLES	♂	20/8/76 (*died 16/10/76*)	Molly X Grumpy
STUMPY	♂	Unknown	ex. Taronga Zoo
MIDGE	♂	Unknown	Caught Carrai, May 1975

There are a number of observations which suggest that the general regard for this species as solitary may be ill-informed. Apart from the experience of capturing a male and female, with five pouch young, only ten feet apart on the same night, multiple captures of Tiger Quolls have been recorded by a number of others. In 1896 Lydekker reported "...the largest, stoutest and heaviest example I have yet seen was caught, in company with five others on Manby Beach, a suburb of Sydney." It has been suggested that there may be a disparity in the sex ratio, with a preponderance of males. Captive litters, however, reveal a ratio very close to 1:1 and it is unlikely that in the wild, female mortality would be higher than that of males. In captivity, males are the more inquisitive and invariably the first to approach and explore new objects placed in their enclosure. If this is applicable to wild animals, a pair approaching a trap would result in the capture of the male, hence the apparently disproportionate sex ratio revealed by capture data.

Like most dasyurids, the Tiger Quoll is largely nocturnal, spending daylight hours asleep either in the nest or basking in the sun. Captive animals (fed in late afternoon) tend to be most active at dawn and dusk and are quiescent during much of the night. The spasmodic nature of their nocturnal rovings seems to reflect differences between individuals and it is likely that free-ranging quolls spend longer periods active in search of food than do their captive counterparts. The effect of food on the activity of caged dasyures may be pronounced and makes it rather difficult to make meaningful, precise statements in regard to their activity rhythms. In Tiger Quolls, small amounts of food seem to heighten the intensity of activity and its duration, whilst satiated animals usually become inactive shortly after feeding. Total withdrawal of food lessens the crepuscular or dawn/dusk nature of the activity pattern and decreases the total activity. These results indicate that the activity of captive specimens may only superficially resemble that of wild individuals.

Dasyurus maculatus has proved to be a seasonal and polyoestrous species, with vaginal smears indicating a cycle 21 days in length. In June/July, 1975 and 1976, both Ann and Molly came into oestrus twice whilst only a single cycle was recorded for Margot in both years. Females are receptive to the advances of males for only three days and during this time become extremely placid and are easily handled. Accompanying this docility, they move about slowly and emit a soft "cp-cp-cp-..." often for long periods of time. This vocalization appears to be an extremely reliable indicator of the receptive period and has only been heard once at any other time. With the sole exception of Stumpy, who showed no interest in females, the introduction of any new male to a cage containing a receptive female was always followed by attempted copulation, successful or not. Females appear attractive to males for a few days either side of the receptive period but amorous approaches outside it invariably result in hostility by the female. Such conflict may be responsible for the killing of females in captivity by newly encountered males.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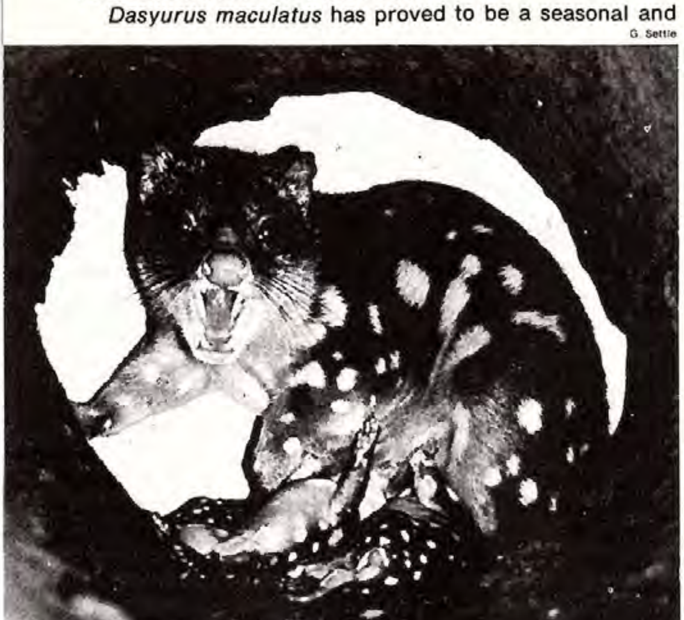
This male tiger quoll is forty-nine days old and is the first to have been born to captive reared parents.

Because of a general housing shortage, animals were kept in pairs or trios of two females and one male. Males however, on approaching sexual maturity and thereafter, fight if placed together. Rather curiously, males do not seem attracted to females with whom they are housed and even in the receptive period, mountings were never observed with such pairings until after the female had been mated by another male. Captive deaths could also have resulted from males attempting to mate with females more than once in succession. Such advances are met with extreme aggression from the female, though she will be happily wooed by any other and then, following her affairs abroad, will again accept the attentions of her former suitor.

On introduction to a new mate, a receptive female Tiger Quoll moves about slowly, pausing now and again with head lowered and rump raised. More often than not her introduction is met with a series of staccato cries by the male, described by one naturalist as "...like a blast on a circular saw...". The semi-continuous "cp-cp-cp" of the female seems to have a placating effect on the ire

G. Settle


Ann with her five young which are seventy-one days old. Tiger quolls defend their young against intruders with considerable aggression.


G. Settle

Climbing-on-back behaviour at eighty-eight days of age. The function of this type of activity is unknown.

of the male and he soon reduces the din to an occasional growl whilst approaching with some caution.

Mating is a protracted affair as in other dasyurids and may last for several hours. The lacerations of the head and neck region of the female, previously described as a product of mating, were not observed by me to be a result of amicable interactions but rather secondary mating attempts in which the female was forced to submit. Although a neck grip typical of many carnivorous mammals including the majority of dasyurids is used, the male often releases it and may gently lick the neck region of the female from time to time. Females usually remain quiet and crouch low with head lowered and eyes half closed.

Some members of the Dasyuridae, including *D. maculatus*, have an appendage to the penis. The function of this auxiliary organ has remained something of a mystery to date. Observations from under a wire-based cage (though the view was far from excellent) were sufficiently clear to suggest that the appendage may in fact enter the rectal passage, thus ensuring the correct placement of the penis in the vagina below.

Unfortunately, only a single captive mating resulted in the appearance of young in the pouch. Even this came as rather a surprise and some time after it was expected. Molly had obviously gone through an additional oestrous and been mated unnoticed. This breeding was, however, the first for captive-reared parents.

Female Tiger Quolls pay a great deal of attention to their young and defend them with considerable malice toward intruders. Because of a general regard for dasyures as cannabalistic species, no chances were taken with the original litter of five and the mother, Ann, was housed separately from the male and reared the young isolated from him. However, as there appeared to be no aggressive encounters between Molly and Grumpy following the birth of their two young, it was decided to allow them to remain together. This was really a calculated risk for it is clearly impossible to make any statements about paternal behaviour in this species if one persists in separating the male parent from his young. The decision proved a good one for at no time were any aggressive encounters observed between Grumpy and either Molly or her daughter Polly. In fact, the reverse was the case; not only was Grumpy seen to groom Polly on several occasions, once free of the teat, but also carried food items such as a rat or piece of rabbit, into the nestbox, dropped it in front of Molly and left to collect something for himself. Prior to the birth of the young, minor squabbles over food items were the most common form of agonistic interaction between adults and were fairly frequent in occurrence. Though normally easy to handle, Grumpy became increasingly aggressive towards intruders, and actually bit one of us on the hand.

G. Settle

Ann's litter at fifty-eight days of age.

An average litter of five is born following a gestation period of twenty-one days. The young grow quickly and at about forty days, spots begin to appear as a result of pigmentation of the still subcutaneous hairs. The young are first able to release the teat at forty-seven to fifty days and gain weight rapidly thereafter. Between fifty and sixty days of age, the infants respond to two cues to locate their mother and siblings. They will approach the adult female when she utters a soft call, "chh-chh-chh . . ." (which is quite easy to imitate) and also curl up and go to sleep against warm objects (even a rock warmed by the sun will do). Both of these responses wane rapidly once the eyes open (sixty-one to sixty-three days) and self-grooming commences with a rather clumsy use of the hind-foot to scratch the head region. As soon as the eyes are open, play in the form of wrestling and mauling begins but it is not until around seventy-one days that any aggression can be observed. Initially this response is only to the sudden and possibly threatening movements of intruders, the young appearing somewhat apprehensive about the situation and

withdrawing from the suspected source of danger uttering cries of "echh-echh-echh...". At this age the young will play with their captors much like a domestic kitten and a curious behaviour dubbed 'climbing-on-back' behaviour is first seen. This action persists until the young are weaned and although it might be thought that this may resemble mounting, both males and females perform it and it bears little in common with that action. 'Climbing-on-back' behaviour does not seem to be related to climbing onto the mother's back either. Whilst other dasyurids frequently carry some of their young with them when they leave the nest, no instances of this were observed in Tiger Quolls; young only climbed onto the female's back within the nest hollow, when they took fright outside or whilst the mother was stationary and accompanied by one or more of her progeny. It was certainly not an approved method of transport.

Social play was well developed by ninety days of age and the young quolls spent much of their active hours chasing, stalking and wrestling amongst themselves and occasionally basked in the sun. The young were now easily startled, would turn to face the transgressor and no longer withdrew from the threat. The original litter were feeding on some meat by one hundred days and weaned by one hundred and twenty but Polly was not weaned until one hundred and fifty days old. It is worth mentioning that Polly, when ninety-five days old, killed an adult mouse less than five seconds after it was introduced to her nestbox even though she had no previous experience with live prey.

Tiger Quolls are not specialized carnivores but rather more opportunistic in their predatory habits. Examination of faecal samples collected in Carrai State Forest during the summer months revealed no fur, apart from the animals' own, and indicated that they had fed on a diet of insects, mainly cockroaches. Winter samples contained rat and rabbit fur and bones, and animals captured at this time were in poor condition and known to scavenge on the carcasses of dead domestic stock. *D. maculatus* appears to be the most advanced of the Dasyuridae with regard to its behaviour and method of attack of large prey. They seem to prefer arboreal routes for stalking and approach, but often come to the ground immediately prior to attack rather than ambushing from above.

Evidence concerning the social behaviour of dasyurids and marsupials in general has been used to make some rather sweeping statements about marsupial evolution and behaviour. Dasyurids being high in the food chain, could be expected to hold many of the answers we seek but only time and further enquiry will tell.

Many persons have rendered assistance over the past three years but mention must be made of R. Williams, R. Whitford, P. Jensen; C. Settle; E. Finney and T. Bergen of Taronga Zoo. My thanks to all. Co-operation of the NSW State Forestry Commission and the National Parks and Wildlife Service is gratefully acknowledged.

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G. Settle

Playing at eighty-eight days of age.

FISHES IN SEAGRASS COMMUNITIES

BY DOUG HOESE

It has long been known that the young of many coastal fishes live in areas or habitats different to those of the adults. This separation of habitats allows a species to use a much greater variety of food resources than it could if the adults and young lived together. Since the very shallow coastal areas are the most productive areas in the sea, it is perfectly reasonable to find juvenile fishes in the most nearshore environments, such as tide pools, mud flats or seagrass beds. Living in very shallow water also gives a fish protection from predation, since most predators are too large to move into very shallow water. However, some predators, such as birds, do feed in shallow areas, and to avoid being eaten, a small fish must either find shelter or be camouflaged. For shelter, a fish may bury in sand or mud, hide under a rock or in vegetation. Vegetation is often a preferred habitat since it is rich in food and contributes to food production as considerable microscopic animal life occurs around and on the vegetation. The decaying plant life is also a source of food for many organisms.

The major widespread vegetation types occur in the sea—algae, such as kelp, and seagrasses, which are true flowering plants. Few studies have been carried out on fishes in seagrass beds in Australia and until recently, most of our knowledge of seagrass fishes came from studies in Japan and North America.

Five different types of seagrasses occur in Australia, but only two types are commonly found in New South Wales, eelgrass (*Zostera* spp.) and strap weed (*Posidonia* sp.). Both grow in brackish and salt water but do not survive long periods in less than about half strength sea water. Studies have shown that some fishes prefer to live in strap weed beds, which generally grow in depths from two to ten metres, but the beds do not appear to serve as major nursery grounds for young fishes. For example, some fishes, such as bream and luderick, live in eelgrass beds when young and then move into strap weed beds.

Eelgrasses (*Zostera* spp.), which grow in very shallow water in depths from less than one to about six metres, occur in many different physical environments, such as estuaries, coastal lakes, and backwaters of harbours. The grass may grow in small colonies or in large beds covering several hundred square metres.

The species of fishes found in seagrass beds in New South Wales vary considerably in their geographical and ecological distribution. About a third of these species are found only in southern Queensland and New South Wales. A small percentage are tropical species, found throughout Queensland, and these species are most common in northern New South Wales. The remaining species are cooler water, temperate fishes, which are widely distributed throughout southern and southeastern Australia. Since eelgrass beds grow in very shallow water, most of the species in the beds are small sized, ranging in size from fifteen to two hundred millimetres. Some of the smallest fishes in the world live in eelgrass beds. For example, the transparent goby, which schools in eelgrass beds grows to a maximum size of twenty millimetres or three quarters of an inch.

The preferred habitat of a species can also vary geographically. A fish may occur in one habitat in New South Wales and live in a completely different habitat in Victoria or Tasmania. For example, the young of trawl

R. Kuiter

Young stages of the variable leatherjacket, *Meuschenia freycineti*, occur in seagrass and algal beds. The colour of the young matches the colour of the vegetation and the young bear little resemblance to the blue and yellow adults, which live in estuaries around vegetation or on rocky reefs.

R. Kuiter

The speckled goby, *Favonigobius lateralis*, is one of several species of gobies which are permanent residents of eelgrass beds. The individual shown here is a breeding female displaying to a male (not shown).

whiting occur in seagrass beds in Tasmania, but it normally lives offshore over mud bottoms in New South Wales. Consequently the discussion that follows is based on fishes in eelgrass beds in New South Wales.

Studies of eelgrass beds in southern New South Wales have shown that eighty to one hundred species of fishes live in the grass beds. These fishes can be broadly classified into three categories, relating to the amount of time spent in the beds and the stages of the life cycle found in the grass beds. The first category comprises resident species, which spend their entire lives in the grass beds. The second group comprises the nursery fishes, which spend only the very early stages of life in the eelgrass beds. The third group comprises temporary residents, which only temporarily utilize the grass beds for feeding or in some cases breeding.

Most resident species are very small sized, ranging from two to ten centimetres. The main resident species are gobies, pipefishes, the fortescue and hardyheads. Although individuals of resident species may spend all or most of their lives in the seagrass beds, few of the species are found only in these beds. For example, the resident goby species may also live on mud or sand flats. Most of the resident fishes live for only one to three years and spawn in spring and early summer in or around the eelgrass beds. Eggs are generally attached to the eelgrass, dead shells or wood and hatch into planktonic larvae, which remain in the water for a few weeks. Resident fishes feed on small crustaceans, worms and other types of small animal life. Some species also feed on larvae, which remain in the water for a few weeks. Little is known of the dispersal of the larval stages. It is thought that the larvae are carried by surface currents for relatively short distances of only a few kilometres before settling into a new eelgrass bed, mud, or silty sand bottom. Once these fishes have settled in a grass bed, they move only short distances and spend the rest of their lives in the same grass bed. Resident fishes feed on small crustaceans, worms and other types of small animal life. Some species also feed on microscopic algae.

Nursery species primarily include species which spawn outside of estuaries, coastal lakes, harbours and inlets. Their eggs are usually shed directly into the sea, but some species attach their eggs to the sea bottom. The eggs hatch within a few days to a few weeks into planktonic larvae, which remain at sea for a few weeks to several months, depending on the species. The larvae then enter the estuaries, coastal lakes, inlets and harbour backwaters, presumably at night on the rising tide, and settle in or around the eelgrass beds. The juveniles then remain in the beds for a few weeks to several months. As they grow, individuals gradually move to the deeper parts of the eelgrass beds, and eventually leave the beds to live over mud bottoms or on rocky reefs. Some species, such as mullet, remain in the estuarine-like environments and return to the eelgrass beds to feed. In New South Wales, the primary nursery fishes are bream, tarwhine, luderick, blue groper, river garfish, variable leatherjacket, fan bellied leatherjacket, yellow finned leatherjacket, old wives, silver biddy, striped perch and several species of mullet. Many other nursery fishes occur in eelgrass beds, but many of these, such as flathead, whiting and snapper are more common on mud or sand bottoms or in association with other types of seagrasses, such as *Halophila*.

Juveniles of some species, such as bream, luderick and blue groper, appear to be restricted to eelgrass beds, while juveniles of a few species occur in several different types of habitats. For example, young of sand mullet are commonly found off sand beaches close to rocky reefs. Similarly, young of river garfish also frequent mud bottoms, while young of old wives occur also in algal beds on rocky reefs. Nursery fishes feed on a variety of plant and animal life.

Temporary residents include adults of species which spend only a short time in the eelgrass beds, to feed, and in a few cases to breed. Normally these fishes are highly mobile and wander over large distances. The species which enter the grass beds to feed, will also feed in other types of habitats and in many cases will normally live close to the beds. For example, the toado, which lives on sand bottoms adjacent to the grass beds enters the beds as the tide is rising or at high tide to feed on animals growing on or around the grass blades. A few species, such as river garfish, lay their eggs in the eelgrass beds. Temporary residents also include species which normally

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Young stages of the old wife, *Enoplosus armatus*, are commonly found in eelgrass and algal beds. The young leave the eelgrass beds after a few weeks and move onto rocky reefs.

do not enter grass beds, such as sharks for which an eelgrass bed is not a preferred habitat. The temporary residents generally feed on small invertebrates or plant life, but rarely on fishes in the beds. Fish predators such as tailor rarely enter the beds; birds are probably the major predators on fishes. However, in many parts of the world, such as Japan, large predators often feed on the resident and nursery fishes.

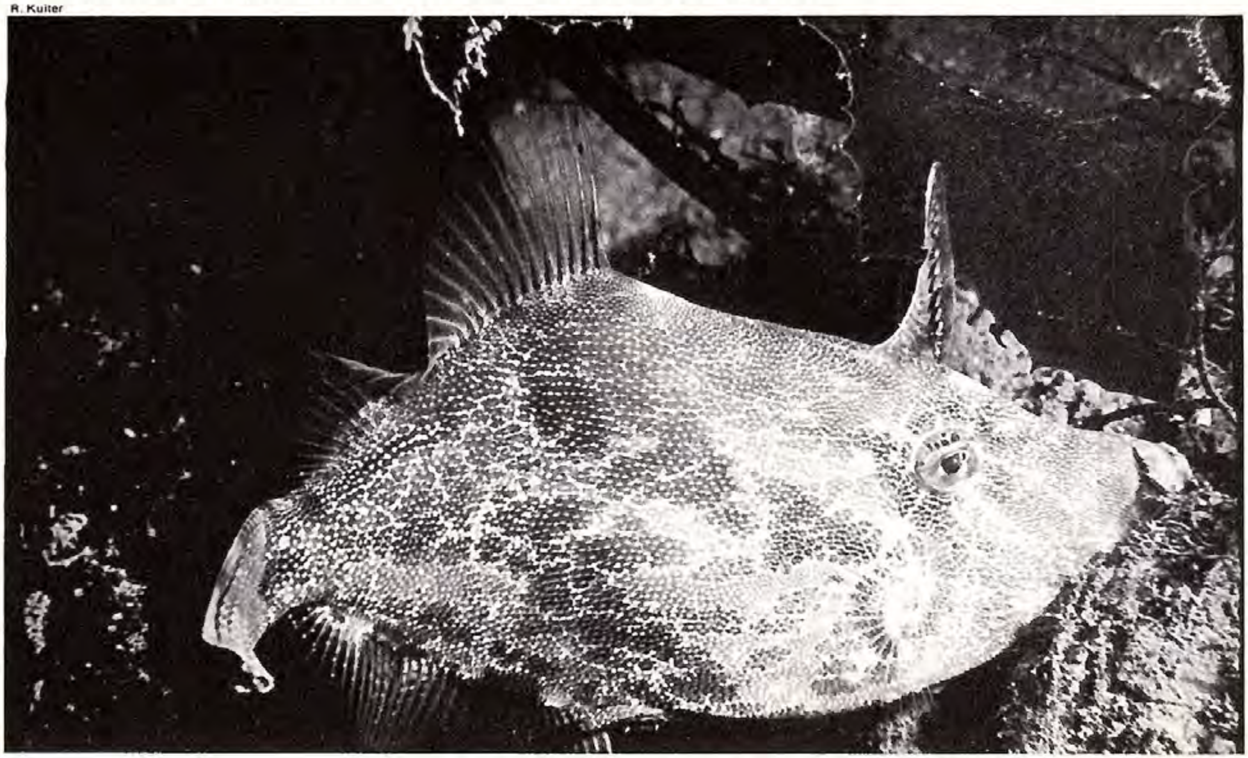
Although populations of fishes in eelgrass beds vary considerably, recent studies are indicating that certain environmental factors affect the abundance of many of the species. In general the abundance of any given species can be related to its spawning cycle and to the growth and condition of the eelgrass.

Recruitment, or settling, of resident fishes from the water column occurs in New South Wales, mainly during the spring and summer months. The massive settlement of juveniles during this period results in these species being most abundant during this period. Gradually over the following months mortality reduces their numbers and they are least abundant in spring just as the spawning season begins. Recruitment of juveniles of offshore spawning species begins in summer and increases in late summer and autumn and extends into winter. They are least abundant in spring and early summer. The longer recruitment period of the offshore spawning species is due to the different breeding cycles of the various species. A few species, such as luderick, apparently spawn over most of the year. While many of the species spawn in summer, some species, such as bream, spawn primarily in winter months.

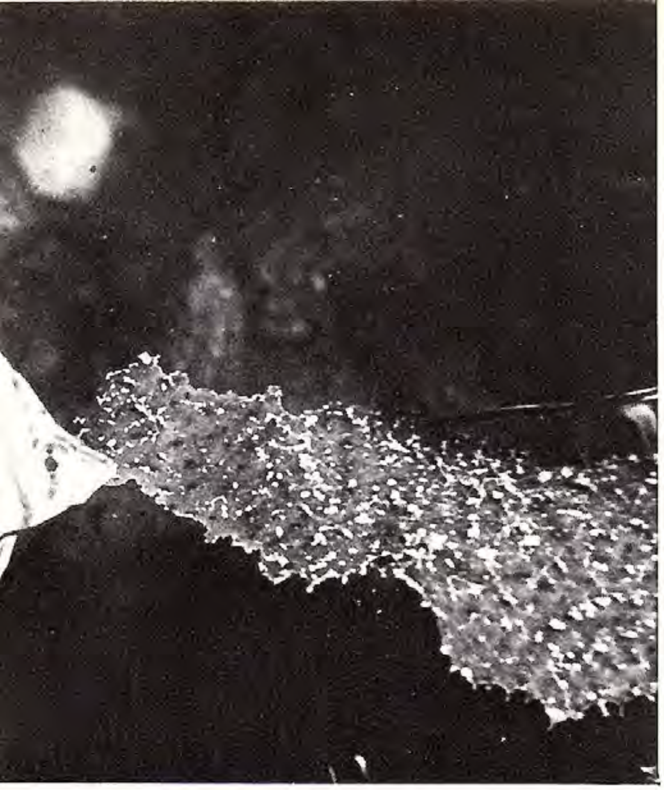
Abundances are also controlled by the sediment type and density and growth form of the eelgrass. Some resident species prefer muddy sediments and others sand, so consequently, the abundances of some of the species will depend on whether the grass is growing on a sandy or muddy bottom. Similarly, when the eelgrass growth is sparse, many species, such as flathead and whiting, which prefer sand bottoms, become abundant in the beds. Normally these species would not be found in dense growth of the grass. The abundance of species preferring eelgrass is highest in dense and tall grass. Caridean shrimps, which live on the grass blades are also most abundant in beds with thick growth, while prawns, which burrow in sand, are most abundant in beds with sparse growth.

The factors which affect the eelgrass are complex and not fully understood. In some areas the beds are most dense during warmer months and in other localities, the grass begins to decline in midsummer. Extensive flooding can lower salinities and deposit sediment in the beds, adversely affecting the eelgrass. In coastal lakes in southern New South Wales, the beds are better developed when the lakes are open to the sea. However, grass beds disappeared after the Gippsland Lakes in Victoria were permanently kept open. It is possible that periodic opening and closing of the lakes are essential for the eelgrass growth.

R. Kuiter



The fan bellied leatherjacket, *Monacanthus chinensis*, is found from eastern Australia to China. In New South Wales, the young stages are found almost exclusively in seagrass beds. Adults live around seagrass or algal beds and often return to eelgrass beds to feed.



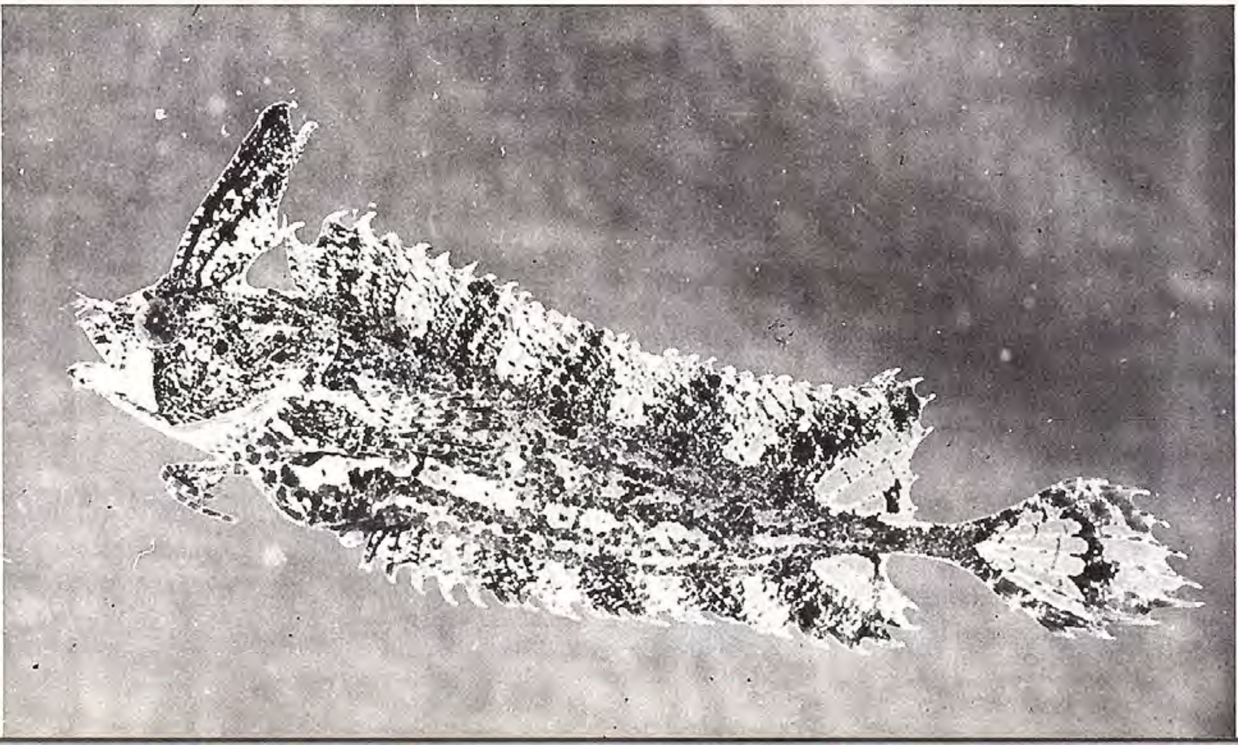
In some seagrass beds the abundances of fishes does not correlate well with the factors discussed above. Many of the factors controlling the abundances of fishes in eelgrass beds are still unknown and considerable research is still to be done.

Because of the importance of eelgrass beds to several species of fishes, and the fact that juveniles of many species are restricted to or most abundant in eelgrass beds, survival of these species is dependent on adequate conservation of the eelgrass beds. Many species such as bream, luderick and mullet, are also commercial or sport fishes. In New South Wales, seagrass dependent species support about a one million dollar a year industry and account for twenty percent by weight of the fish catch. The eelgrass beds also serve as a feeding ground for many other estuarine dependent species whose survival and abundance is dependent on environments in estuaries, inlets, coastal lakes and harbour backwaters. About thirty to forty percent of the New South Wales prawn and fish fisheries is based on estuarine dependent species.

In many areas of southeastern Australia, eelgrass beds have declined considerably over the last thirty to forty years. In some cases, such as in Port Hacking, the eelgrass has been replaced by strap weed which is not as important as eelgrass as a nursery ground. It is thought that much of the eelgrass destruction has resulted from man's activities. Destruction of eelgrass beds can result from natural causes but little information is available to document man's effect on the seagrass beds. However, studies carried out overseas have identified several factors which can have adverse effects on the eelgrass. It is thought that clearing of land around catchment areas has increased sediment runoff from the land, resulting in deposition of coarse sand in many estuaries which creates an environment unsuitable for eelgrass. Construction of dams along rivers in the southeastern United States has reduced the freshwater inflow into lagoons, causing them to become too salty for many kinds of fishes and prawns. It is thought that dam construction in Australia may substantially reduce nutrient transport to the grass beds, adversely affecting the grass. Closing of coastal lakes can in some cases result in lakes becoming fresh, killing the grass beds.

There is an increasing need for studies to be carried out in Australia, since the grass beds are rapidly coming under human influence. While overseas studies are useful, environmental factors may not necessarily be the same, and the species found in eelgrass beds in Australia, although related to overseas species, are different. Rainfall fluctuates considerably over long time periods in Australia, a situation found in only a few other areas, such as Africa. Probably the greatest threats to eelgrass in Australia are pollution, land development along the shores of estuaries and coastal lakes, and dredging, all of which can lead to physical destruction of the eelgrass beds. It is ironic that many of these activities, which provide facilities for sport fishermen, may eventually lead to reduction of the sport fishes.

G. Allen



The crested weedfish, *Cristiceps australis*, is a common adult resident of eelgrass beds. It is a highly camouflaged species, with its colour matching the colour of eelgrass or the algae in the beds where it lives. It is only found in vegetation.

S. Startin

In July of 1974, and again in the following year, we visited the Indonesian island of Roti, off the southern tip of Timor in the Lesser Sunda Islands (Nusa Tenggara). Our initial intentions were to study the traditional weaving and *ikat*-dyeing techniques, and to collect examples of the highly individual Rotinese weaving. Although we were witness to a period of cultural transition in which new technology was rapidly beginning to undermine and supersede the old ways, we became increasingly aware of the close link between the women's weaving activities, and the natural cycle of the seasons.

All of the weaver's tools, spindle and loom, are made from local woods and bamboo by *tukang* (specialists), or by her father or brothers. Her raw materials are cotton and locally gathered mordants (dye fixatives) and dye stuffs. Cotton trees were once widely cultivated for handspun thread, but now imported yarn is more common. Its smoothness which allows for greater clarity of design, actually adds to rather than detracts from the feel and look of the cloth. The women weave on two-beam frameless backstrap looms and create intricate designs in three-, four-, and sometimes even five-colour combinations by *ikat* or tie-and-dye of the warp over repeated dyeing sessions.

The *ikat* method of dyeing is found throughout Indonesia, and it is especially characteristic of the textiles of the Lesser Sunda Islands. Roti is the southernmost island of the group. Each of the islands has preserved a unique style of decoration, even though the basic method and the natural dyes are constant from island to island. On all the islands, the decorations incline towards small rounded forms, curvilinear motifs and linear arcs. These shapes are exactly those that are the most difficult to achieve by the *ikat* technique, because all lines except for stripes must be rendered in small steps. Precision of line and exactitudes of detail are prized above all. It is a challenge to all weavers using the technique to overcome its limitations and create the stylistic effects desired—Rotinese weavers accept this challenge eagerly.

Within the relatively rigid traditional framework of technique and colour variation, in themselves determined by the available local materials, there is considerable creative experimentation with design motifs. This improvisation of motifs seems to be unique to the Rotinese craftswomen, amongst the Lesser Sundas group. Although some of the motifs appear to have remained unchanged since the Dongson period, more than two thousand years ago, other designs are formed spontaneously through an individual weaver's experience. These innovative patterns are completely valid as they are interpreted in the traditional manner with the established colour sequences and have lost none of the strength and vitality of the ancient motifs. We felt that

WEAVING WITH NATURE

BY DEBORAH JARVIS AND SUZANNE STARTIN

this adaptive ability of Rotinese weavers makes them exceptional among the weavers of the eastern Indonesian islands.

The women of Roti span the changing seasons with their craft, following closely the yearly cycle of nature. In the season of the east wind, February through March, the cotton tree flowers. The rainy season is coming to an end, and in the succeeding dry period, the cotton pods burst, allowing the balls of white fibre to be gathered for spinning. Little baskets of white cotton rest on the thatched roofs to dry. The work is slow. Picking out the hard black seeds, teasing the cotton fibre by hand, then with a wooden spindle, spinning fine thread. At the height of the dry season, women go out to gather the herbs, roots, barks and shells necessary for the preparation of a mordant. To assist her during her work, each woman prays and makes offerings to the ancient deities of the trees and rocks.

It is important that the dry season is not broken by rain as rainy weather during the mordanting process will cause the cotton to rot. The eight ingredients of their mordant, *loba* bark, *kemiri* nut, *borocundu* leaves, *metomata* root, *relas* bark, the *nitas* fruit, *menomudu* and papaya roots are crushed and ground in a heavy wooden mortar then soaked with the ashes of burnt *kusumbang* wood and bonitas shells. The skeins of cotton are entered into the prepared solution and boiled twice a day for three days, drying between subsequent daily boilings. In this way, the capacity of thread to receive and hold colour is greatly improved.

The mordanted thread is used for both warp and weft. Only the warp is *ikatted* or tie-dyed to achieve the design while the weft is dyed the basic background colour, usually a deep indigo blue, sometimes a rich rust-red. The designs are not the result of a weaving process, but of the *ikat* technique.

As the rainy season approaches, the weaver works on her warp, preparing it for the tie-dyeing: the warp thread is wrapped continuously between two beams set apart at half the length of the cloth, in a rigid framework. The whole frame is either laid on the ground or stood on an angle like a blank canvas.

The threads in a warp number approximately forty to the inch so that for a cloth to be one metre wide, almost 1500 windings of the warp thread onto the frame would be needed. The length and width of the warp are determined by the intended size and function of the cloth. Because of the narrow structure of the backstrap loom, for a cloth wider than eighteen inches, the width of the warp is made up of two sections of warp threads—woven separately after the tie-dyeing process is completed—so that the final cloth consists of two matched woven halves, joined with a seam. There are five traditional garments; the women's *sarong*, a long tubular skirt folded and tied at the waist, the women's shawl, head scarves worn by both men and women, and the men's *sarong* and shoulder cloth or *selimut*. It was once customary for women to weave their husbands a *selimut* with an individual central motif so that he could wear it folded on his shoulder as a personal insignia.

Rain falls occasionally. The women now have more daylight hours free to begin the *ikat* process, for this is an exacting and time-consuming step. First of all, the warp on the frame is separated into sets of six threads, each of which form the basic unit for tying. Strands of raffia-like straw are then pulled through beeswax to make a dye-resistant binding. Then work begins, binding up one set of six threads at a time, to create the pattern: the design is built up from tiny bound rectangles in a step-on-step manner.

Because the warp is doubled on the frame, the weaver binds the design onto the combined layers, so that the finished cloth is two mirror images separated by a plain undecorated space where the thread was passed over the end beam during the *ikatting* process. (The opposite end, also undecorated, is cut when weaving is completed and, in shawls and *selimut*, becomes the fringe; in *sarongs* it is the selvage edge). In this way, large areas of warp are more quickly tied off. The areas to remain white in the decoration are tied off first. Each set or primary element is tied over several times with the dye-resistant straw, which is then cut with a small knife. *Ikat* becomes surprisingly quick as the deft fingers move surely over the warp, securing those areas that will appear white in the final design.

It is now August or September and the long dyeing process can begin. *Mencudo* root is gathered and carefully stored. It is a long, thick root which, when properly prepared, gives a rich rust dye over successive soakings. If the cloth is to include small elements of yellow, those areas to be dyed rust-red are tied off and the first dye-bath is prepared from pounded tumeric root or *kunyit*. After this yellow dyeing, the warp is dried and the yellow sections tied to resist the subsequent blue and red dyebaths. At this point, *tauk* must be gathered and prepared. This insignificant looking little plant, *Indigofera*, springs up during the rainy season. It was once widely cultivated as a dye stuff on Roti, but now careful cultivation is not common. The growth of the *tauk* gives fresh impetus to the women at their *ikatting*. It must be

DEBORAH JARVIS is a New Zealand weaver with a special interest in the *ikat* technique. Together with SUZANNE STARTIN, an Australian art teacher and potter, she visited the Indonesian islands observing and researching traditional weaving, particularly on the island of Roti. They made a collection of Rotinese weavings, examples of which have been acquired by The Australian Museum.

A traditional *selimut* from the Nembrala district showing the finished design and rich colours achieved through the *ikat* technique.

used freshly cut, so the possible period for obtaining the deep indigo blue is short and seasonally defined.

The blue coveted by the women is only gained through successive dippings. If they want to include a small element of green in the design, yellow areas are dyed once in the *tauk* dyebath to produce green and then tied off. A clear apple green results from this overlay of blue on yellow. The remaining warp is then dyed repeatedly until it has taken the desired depth of colour. Only the fringe end, like a handle, is excluded from the dyebath because it will be dyed red in the *mencudo* dyebath. Last of all, the gathered *mencudo* roots are pounded with a pestle in a huge mortar. Five soakings are needed for the rich red which is valued for its deep, saturated quality. Once prepared, the areas to be dyed red are untied and those that will remain blue are tied off. Now the entire warp is immersed in the prepared bath. After five successive soakings and boilings the deep red is obtained.

Once the sequence of the design is established, the women no longer return the warp to the *ikatting* frame when tying off sets between dyebaths but work on the hanging bundle of warp. As the weaver works, the complete design evolves in her mind. She conceives of the pattern without pen or paper, using the map of her memory, or an already woven cloth with design motifs particular to her own family or district, or perhaps images derived from the sea, sky and land around her—new motifs that she will strive to express in the cloth. Although the *ikat* technique imposes few restrictions on the composition, the difficulties and complexities of tying increase in direct ratio to the number and variety of motifs and the differences in colour. Each motif, each variation in colour calls for new sets of relationships in the tying process. Whether the weaver chooses to *ikat* a traditional design, or to innovate her own motifs depends on her personal skill and experience.

After the final dyeing, the dried warp is carefully lifted by two women onto the warping frame where all the bindings are removed. The end beams of the frameless backstrap loom are inserted, and the warping frame dismantled while two helpers maintain tension on the warp. Then, seated before her loom with the backstrap firmly in place over the small of her back, the weaver inserts the needle, shed sticks and beater. A narrow bamboo sliver is sewn into the warp to act as a base upon which the first rows of weaving can be beaten. The beater is made from a handsome close-grained dark wood which is worked to a satiny smooth patina. The breast beam is formed from two close-fitting pieces of wood, which clamp the warp tightly as the weaver leans on her backstrap to put tension on the loom while she weaves.

Weaving proceeds with a bamboo hand shuttle in a simple warp-faced weave. There are more warp threads than wefts to the square inch so that the undecorated weft is not seen on the surface of the cloth. As the woven cloth grows, the circular warp is moved round the loom so that the unfinished warp is always within easy reach of the weaver's hands. By this time the cotton tree is flowering once again. During the daylight hours in the sheltered outer verandahs of their houses, the women work at their weaving, carefully readjusting the warp threads as they go, anxious to maintain the clarity of their design. Only when the weaving is completed and removed from the loom is the fringe or the *sarong* seam cut. At each edge, where the woven area meets the fringe, two threads are twined to prevent fraying. The meticulous weaver puts the finishing touch to a *selimut* by rolling the fringe threads about ten at a time into cords, so that the fine fringe does not mat or tangle in use. As the days grow drier and the cotton is ready to pick, the women of Roti will be out gathering the white fibre and spending their evenings teasing and spinning the cotton in preparation for the next year's cloths—the year has turned full circle.

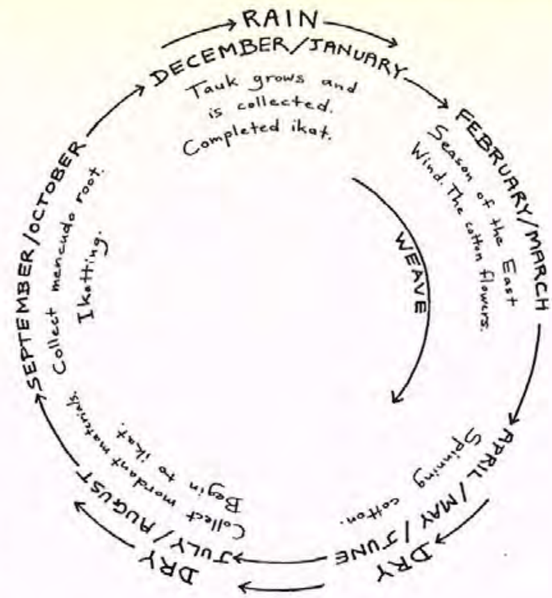
In a two-year period, working intermittently and seasonally a woman may only complete two *selimut*. Other women who supplement the family income by sales of their weavings may produce three or four cloths in the span of a year. Until quite recently, knowledge and aptitude in the art of weaving were considered essential for a girl to reach marriageable status. Spinning was the first skill a young girl mastered, and when she was fourteen or fifteen years old, her mother would teach her to weave, and to create the traditional *ikat* designs.

Now as times change, this formerly indispensable prerequisite to marriage is being forgotten. As a result, certain areas of Roti are developing as weaving centres. Women in these areas are maintaining the traditional weaving and dyeing techniques and will weave on order for people from other districts who require ceremonial cloths for special events—marriages in particular. One group of islanders, the N'dau, who live in B'aa, the port town of Roti, rely on their work for an income from sales in nearby Timorese markets, but in order to sell in quantity, they have adopted chemical dyes and simplified designs. Their weavings are inferior to the traditionally woven textiles; the motifs are clumsily executed and the colours fade quickly. To their credit, the Rotinese discriminate against this poor quality cloth.

The coming of Christianity to Roti has also had its effect on the weaving; at times bringing tenacious old beliefs into conflict with Christian dogma. In one village women stopped work altogether for eight years because a visiting preacher forbade adherence to the animist rites and prayers associated with their craft. Weaving has begun again with new vigour since an understanding has been reached, whereby the women can still pacify the nature deities without compromising their Christianity.

We left Roti for the last time just as the rains were beginning. Women were bringing *mencudo* roots to wash clean in the streams, and *ikatting* in preparation for the growth of the *tauk*. Their pride in their craft is evident; there is a Rotinese saying that the character of a woman is revealed in her weaving. Although it is no longer essential to be a competent weaver before marriage, Rotinese society still sanctions and openly approves of women who are artful weavers. On this dry and stormy island, their weavings bloom like strange exotic flowers. At each major life event, the Rotinese adorn themselves in their beautiful cloth which, at death, becomes a most fitting shroud. The women of Roti are weavers who give expression to the relationship of their hearts with nature through the warp and weft of their unique and beautiful cloth.

S. Startin



CYCLE OF SEASONS AND WEAVING

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Above: The warp threads are bound in readiness for the final red dyebath.

Below: The cloths as worn by men and women in the traditional manner.

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bove: Ibu Dehla shows the spinning of local cotton with a wooden spindle.

elow Far Right: As the cloth is woven 1 the backstrap loom the warp is care- ılly adjusted to maintain the clarity of the *ikat* design.

elow: Bundles of *ikatted* warp threads anging up to dry and completed warp threads assembled on a frame after removal of the bindings.

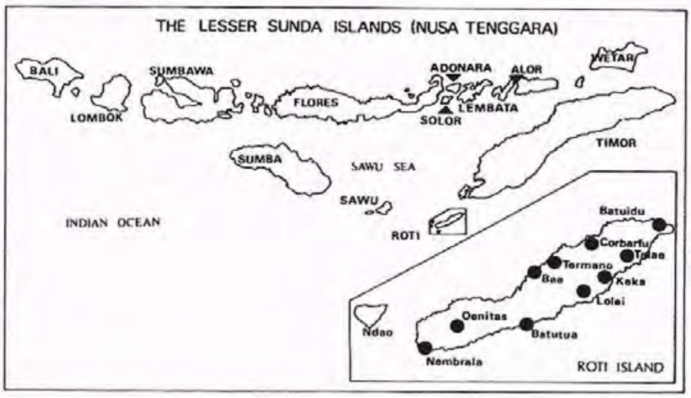

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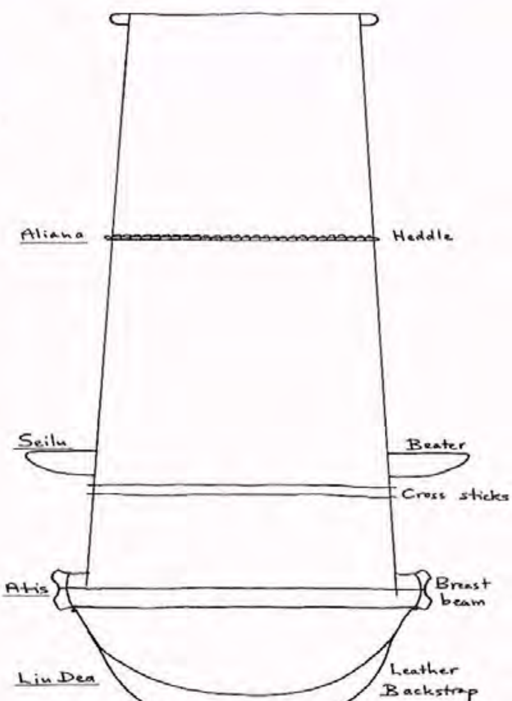
DIAGRAM OF BACKSTRAP LOOM



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