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Part 1

**1.—Variation, Classification and Evolution in Flowering Plants—
with particular reference to *Thysanotus***

Presidential Address, 1961

By Norman H. Brittan, B.Sc., Ph.D.*

Delivered—17th July, 1961

The sources of variation in flowering plants are briefly discussed and illustrated by examples from the genus *Thysanotus*. In two species—*T. patersonii* and *T. tuberosus*—evidence of variation is presented which supports the establishment of sub-specific taxa. The occurrence of intra-specific polyploidy is reported and compared from the point of view of geographical distribution with other selected Australian genera.

The world distribution of the tribe Asphodelae in terms of its constituent genera and the distribution of the species of *Thysanotus* are considered in the light of Willis' Age and Area theory and of a recent hypothesis of Smith White. A hypothetical evolutionary history of the genus *Thysanotus* is presented.

This address will be concerned with plant systematics and will indicate the various lines along which research into what may in general be called "the species problem" has been conducted and how the results from such investigations have affected the science of flowering plant taxonomy and thrown light on pathways in evolution.

In systems of classification of flowering plants there had grown up from the time of Linnaeus (1753) the idea that each individual species was an invariable entity and out of this concept arose the use of the "type"—a single plant specimen located in some particular herbarium which provided a fixed reference point and which, taken in conjunction with the written description of the species, enabled subsequent workers to identify plants of the particular taxon. This may be an unfamiliar word to some of you—it means a particular taxonomic entity at whatever level is under discussion, for example—species, genus, etc.

Over the last thirty years concurrent with the rise of genetics as a science there has been a marked increase in the interest taken in variation in plants and as a result there has developed what has variously been called the "new systematics" (Huxley 1940), "experimental taxonomy" (Clausen, Keck and Hiesey 1941) and "biosystematy" (Camp and Gilly 1943). The results from such investigations have not so far resulted in a change in the orthodox taxonomic

methods nor in a rejection of the type system, although various authors as for example Gilmour and Gregor (1939) and Gilmour and Heslop-Harrison (1954) have suggested a nomenclatural system which would assist in codification of the various categories among plants recognised as a result of experimental taxonomic investigation.

The point of departure between what has been called "classical" or "alpha" taxonomy and experimental taxonomy is the attention paid to the variability of the plant species as a result of intrinsic and extrinsic factors. The interrelationship of the two approaches is shown in Table I modified from Heslop-Harrison (1953).

In order that we may better understand the relationship between these two approaches let us look first at some of the sources of variation in the flowering plant. Most people are familiar with the basic cell of which the complete structure of the plant is made up. It is a complex assemblage of inorganic and organic chemical compounds in an aqueous medium contained within a membrane enclosed by a cellulose cell wall. Among the important organic chemical compounds are proteins, ribose nucleic acid (RNA) and desoxyribose nucleic acid (DNA). The proteins are important because of their part in building the fine structure of the cell and their association with the enzyme system. Together with the nucleic acids just mentioned they form nucleoproteins of which DNA-proteins make up the genetic units of the cell—the chromosomes—which can be made visible by suitable methods, and RNA-proteins make up microsomes in the cytoplasm and also form other so far invisible (except in the electron microscope) cytoplasmic bodies. Genetics has established that the chromosomal part of the genetic system is distributed in a regular fashion by meiosis prior to the formation of embryo sacs and pollen grains and that at this stage in the life history there is the possibility of variation in the genetic constitutions of the various products of meiosis. Here then we have the first method by which variation can occur.

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TABLE I

The relationships of "classical" and "experimental" taxonomy (after Heslop-Harrison 1953)

	CLASSICAL TAXONOMY	EXPERIMENTAL TAXONOMY
AIMS	Description, classification and naming.	Identification of evolutionary units, determination of genetical relationships.
UNIT OF STUDY	Individuals, usually dead.	Breeding population, or a sample from it, living.
SYSTEM OF CLASSIFICATION	Basic unit the species, fitted into a hierarchical system.	Classification not the primary aim, basic units vary.
SOURCE OF DATA	Morphology, anatomy plus notes on flowering time and geographical distribution.	Morphology, anatomy, karyology, life cycle details, effects of habitats, genetical tests.
TESTS OF CHARACTERS	Intuition and trial and error.	Statistical methods.
METHODS OF DESCRIPTION	Individuals and "type" concept.	Populations or samples of populations.
CONCEPT OF NATURAL VARIATION INVOLVED	Essentially static, assumes continuity of form within species.	Essentially dynamic, internal variability of sexual populations is recognised, adaptive nature of much population differentiation acknowledged and made deliberate object of study.

Whether the process of meiosis always results in variation depends upon the genetic state of the organism, whether it is homozygous or heterozygous and also on the breeding system of the plant. With regard to the latter there are three possibilities, (1) inbreeding (or self-pollination), (2) outbreeding, or cross-pollination) and (3) apomixis—a single term covering a number of possible variants of the sexual process. To deal with the last of these first—apomixis is a mechanism which results in the elimination of variation resulting from meiosis and conversely the maintenance of variation occasioned by means other than meiotic recombination. An extreme form of apomixis is the replacement of sexual reproduction by vegetative propagation.

To return to the first two, the choice between in- or out-breeding may be controlled by either the floral morphology of the plant or a specific part of its genetic make-up, or possibly both. As an example the pea flower is anatomically designed for self-fertilisation since the stigma is receptive at the time of anthesis, and also in close proximity to the anthers. The cleistogamous flower of the violet—since it never opens—also ensures self-fertilisation. On the other hand distylous flowers—types of flowers which are found with two possible lengths of style alternating with two possible anther positions—are spatially arranged to encourage cross-pollination by insect visitors as for example the primrose (*Primula*) and loosestrife (*Lythrum*). In some of these cases the anatomical mechanism is reinforced by a genetical system of incompatibility genes.

Of anatomical mechanisms for ensuring cross-pollination may also be mentioned the system in some members of the Compositae (the daisy family) in which pollen is shed into a central tube and released to visiting insects as a result of the style growing up through the tube. When the style has grown beyond the limits of the tube the divided apical parts of the style recurve and expose the inner receptive surfaces of the stigma which then becomes receptive to other pollen. Genetic systems for ensuring cross-pollination are based on the "S" gene series which, by means of interaction between

pollen carrying a specific allele of the series and diploid stylar tissue carrying the same allele results in retardation or complete inhibition of the growth of the pollen tube or even inhibition of pollen germination upon such stigmas. Other methods are known which achieve the same end as for example in the evening primrose (*Oenothera*) in which both ovules and pollen grains containing particular genetic combinations (the so-called Renner complexes) do not develop. This is a system of gametic lethals; alternatively where particular zygotic genetic combinations do not develop, a system of zygotic lethals is found.

What then can be said from the point of view of variation about the results of the various breeding systems just mentioned? Apomixis will tend to reduce variation, or if variation results from mutation it will perpetuate it without change—it is therefore a system which imposes restrictions upon the variability of the plant possessing it. Obligate self-pollination will result in homozygosity after relatively few generations, since from inbreeding a heterozygote followed by self-pollination of all the progeny (neglecting any form of selection for a particular genotype) the proportion of heterozygotes: homozygotes becomes progressively 1:1, 1:3, 1:7, etc. Put in another way the proportion of heterozygotes in such a population would be represented by $(\frac{1}{2})^n$ where n number of generations of inbreeding. We see in this a very rapid reduction in the number of heterozygotes in such a population. Only with outbreeding is there the possibility of segregation and recombination and thus the persistence of heterozygosity. We therefore expect that the self-fertilised species will possess little or no genetic variation within its populations derived from a single individual whereas the outbreeding species will show marked variability.

So far we have been concerned with genetic variation, which is controlled by the chromosomally-borne genes. The whole chromosome complement of the plant may be altered by the incidence of polyploidy—in the simplest case the duplication of the chromosomal set to produce a tetraploid. This increase in chromosomal material may or may not show itself in the

morphology or physiology of the plant. There is a great deal of literature now available on this topic and one may generalise to the extent that increase in size of various parts, for example flowers, frequently coupled with reduction in fertility, often occurs following polyploidy.

Variation may also arise from environmental factors. This was thought at one period to be the reason for the identity of allied species and claims have been made that by transplanting individuals from their normal habitat to another they could be shown to be transformed into another species typical of the new habitat. The experiments of Bonnier (1895) were claimed to show the transformation of lowland species into alpine ones. Due to lack of careful cultivation methods and keeping of accurate records, the results from these experiments are now viewed with suspicion. Subsequently the transplantation technique has been used by such workers as Turesson in Sweden, Gregor in Scotland and Clausen, Keck and Hiesey in California. Not only have reciprocal transplants been used, but the concept of growth under uniform environment of plants from diverse ecological situations has been extensively used. The use of this approach under most critically controlled conditions has been in the use of what have been termed "phytotrons"—each consisting of a collection of rooms with either natural or artificial lighting in which strict control of day and night temperatures, humidity and day length is possible. Under such conditions it has been shown by Went (1953) in the case of the Earhart Laboratories in California that variation due to environment can be virtually entirely removed and that as a result genetical experiments which would normally require many replications to ensure statistical accuracy can be conducted with very few plants. This type of apparatus provides an ideal site for researches into physiological differences between races of plants as for example the work of Hiesey (1953) on *Achillea*.

The sources of variation have now been mentioned, but what of their effect upon the plant species? Genetic variation may provide sharply discontinuous morphological changes as for example in flower colour. A very common example of this is the mutation to white flowers in a species normally possessing coloured flowers. In *Thysanotus* this has been found in several species, e.g., *T. triandrus* (Shearer, personal communication), in *T. tenuis* near Tinkurrin, Western Australia, and *T. tuberosus* at Virginia, Queensland. In most cases the change to albinism is complete and affects all parts of the flower. In the case of the Tinkurrin plants however, there seem to be two stages each presumably controlled by a separate gene. In one of these the anthocyanin pigment is absent from the perianth parts but remains in the anthers (which in this and most other *Thysanotus* species are normally purple coloured); in the other, anthocyanin is absent both from perianth and anthers, the latter then appear green. Mutation of the normal pale purple flower colour to a salmon pink has also been seen in a population of *T. tuberosus* in southern Queensland.

A presumed mutational effect which concerns the morphology of the perianth in *T. patersonii* is reported from localities in northern South Australia and southern Northern Territory. In this case the fringed margin to the inner perianth segments is absent and led Black (1943) to use the manuscript name of var. *exfimbriatus* for such plants. Live material has recently been obtained from a population of this plant through the courtesy of Mr. Paul Wilson of the South Australian State Herbarium and it is hoped in the forthcoming season to be able to determine whether environment changes the expression of this character. By experimental cross-pollination with normal fringed types it is hoped to be able to determine the genetical relationship between the normal and the ex-fimbriate form.

Genetic variation may also result in continuous as opposed to discontinuous morphological variation giving the so-called quantitative variation shown mostly in characters such as the overall size of plant parts. This aspect of plant variation has been extensively studied by the Californian workers Clausen, Keck and Hiesey (Clausen 1951). The results shown in Figure 1 are a sample of the type of results obtained when plants from various localities on a transect across California are grown under uniform conditions at the Carnegie Institute experimental plots at Stanford, California. Each plant shown in the figure represents the mean of the population from that locality and the histograms show the variation within that population. If individual plants from such populations are selected and vegetatively propagated by means of ramets and grown under identical conditions at each of three localities, results such as those shown in Figure 2 can be obtained. This shows that the responses of genetically different plants are quite different at the three localities and that among the vertical lines of plants which represent the ramets derived from a single individual, there are marked differences in the response of the plant to the environment at the three localities used in the experiment. At any one particular habitat the sum of the variation adds up to the total variation shown by the histograms in the previous figure.

As a result of these approaches together with experimental crossing of races from different geographical and ecological habitats it has been possible to elucidate the genetical and physiological bases for the observed morphological differences among members of a particular species.

As yet no extensive experiments of this sort have been carried out with *Thysanotus*—some transplanting to a more or less uniform environment in a Perth glasshouse has been undertaken and progeny have been raised from seed derived from selfed parents. From the latter the indications are that there is little variation in such characters as size of plant within the progeny. This lack of variation in sexually produced progeny would lead one to suspect that the plant was most likely to be normally self-fertilised in nature.

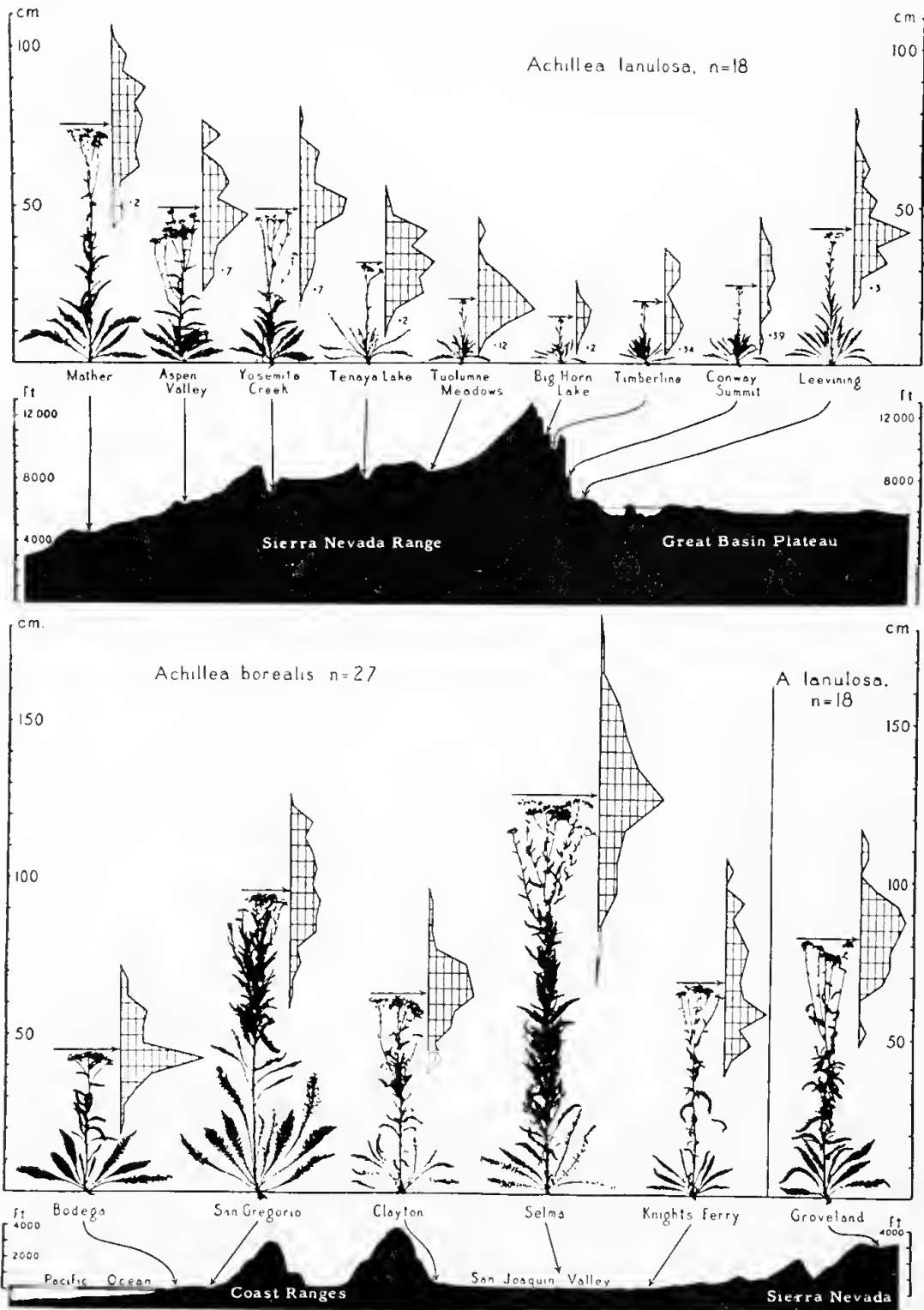


Fig. 1.—Altitudinal climatic races of *Achillea* from a west-to-east transect across central California. The frequency diagrams indicate variation in height within the populations in the Carnegie Institution plots at Stanford, California. The plant specimens represent the means. (after Clausen, Keck and Hiesey 1948.)

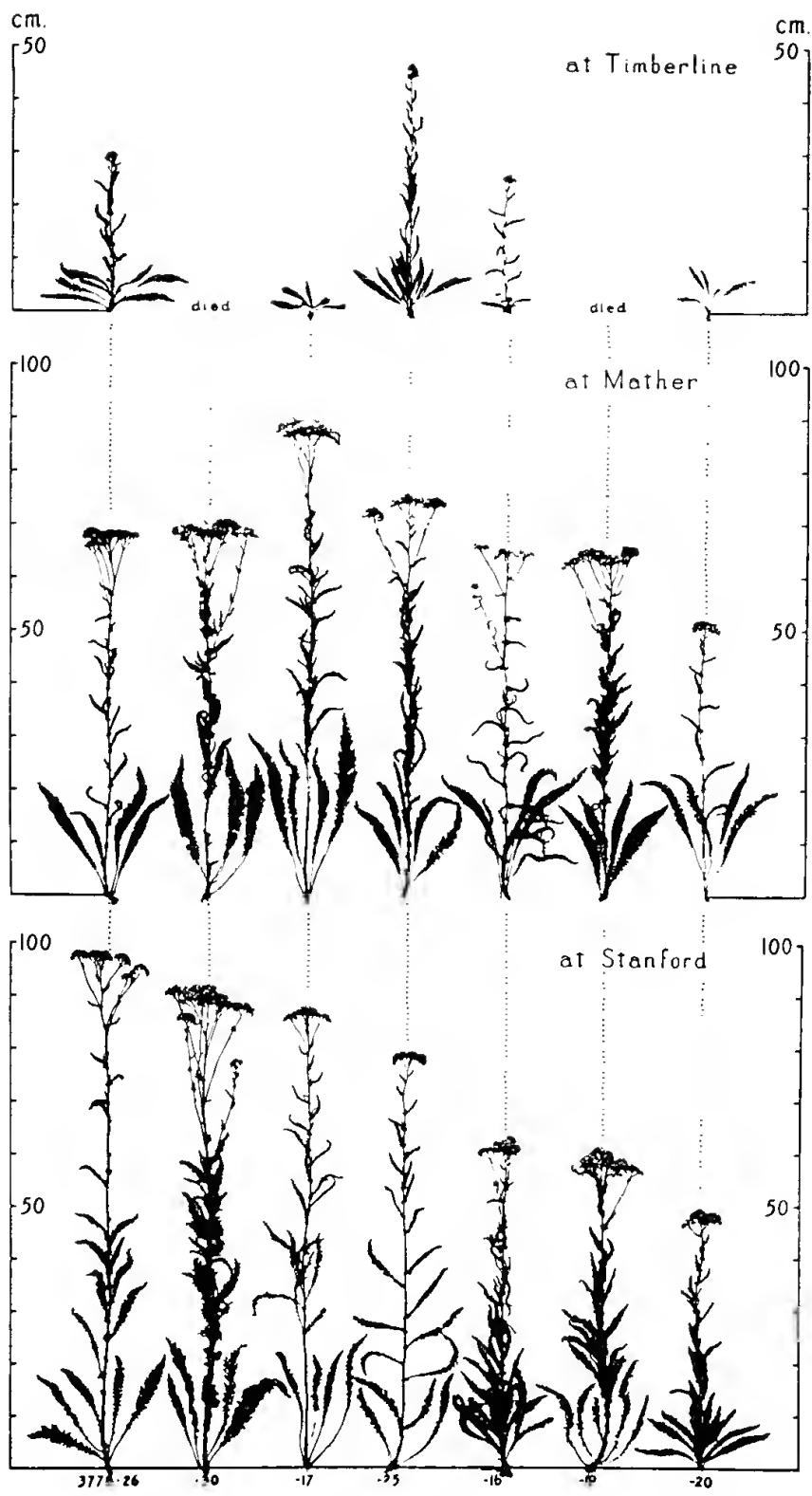


Fig. 2.—Responses of seven cloned individuals taken from a population at Mather (alt. 4,600 ft.) when transplanted to the environments at Stanford, Mather and Timberline. (after Clausen, Keck and Hiesey, 1948.)

Here we may make a digression to look at the floral morphology of the plants. The flowers are either three or six stamened and typically the anthers are curved and tend in the open flower to lie with their apices near the terminal stigmatic part of the style. In the majority of the species the anther opens by a terminal pore and it is thought that there is a "pepper pot" pollination mechanism in these cases. Such a mechanism does not provide large quantities of pollen loose in the flower. In a few species the anthers open by longitudinal slits and in these cases there is much more pollen freed at any one time. In these latter cases also there is close proximity of style and anther and pollination by direct mechanical transfer of pollen is suspected. Insects are hardly ever seen visiting the flowers and emasculated non-bagged flowers in a glasshouse in the vicinity of other open non-emasculated flowers of the same species do not set seed. The evidence therefore suggests self-fertilisation as the normal condition for the plant.

If instead of considering variation in height on an intrapopulation basis we look for inter-population variation within the species we find examples of this in *T. triandrus* and *T. multiflorus*. In the former species the variation was such that Domin (1913) erected a series of varieties of which the smallest—from the vicinity of Youndegin (35 miles east of York, Western Australia) had been given specific rank by Ewart and White (1908) as *T. bentianus*. If these variations in height are plotted geographically a positive correlation appears between decrease in height and decrease in annual rainfall. It would seem that in this case we have a cline—defined as a gradual transition in a characteristic associated with geographical or ecological change. A similar pattern emerges from a study of height in *T. multiflorus* which shows reduction in size correlated with progressively south-western distribution. These variations may be merely plastic responses to the environment, this can be proved or disproved only by determining whether the height typical of the original population is maintained when plants are grown under more or less uniform conditions. If changes of environment do not bring about changes in the height of the plants the genetical control of the character is demonstrated. If it is possible to select types morphologically different from others in the cline the term ecotype of Turesson could be applied to such plants. Ecotypal variation implies that genetic modification has occurred in response to the environment with modification in some characters as for example size, but not to the extent that the plants showing this variation should be placed in different taxonomic groups. The work of Silsbury and Brittan (1955) demonstrated the existence of ecotypal variation in *Kennedyia prostrata*.

As a general rule it is to be expected that if a species covers a wide geographical range, which is therefore likely to include several different ecological conditions together with the possibility of isolation into small populations there is greater likelihood of the development of infraspecific categories. In *Thysanotus* the two most widely ranging species are *T. tuberosus*

and *T. patersonii*. The former has a distribution which ranges from Cape York and northern Northern Territory through Queensland, New South Wales, Victoria and to the east of the Mount Lofty Ranges in South Australia. The typical form over this range has flowers with perianth segments 11-19 mm long, six stamens—of which three have short (3-3.5 mm), more or less straight anthers and three with long (6-9 mm) curved anthers. The longer ones are comparable in length to the style. This floral morphological pattern is constant over most of the range but may be accompanied by variation in overall size and vigour of the plants. In the area around Brisbane and possibly south into New England there occurs a distinct form with perianth parts 7.5-9.5 mm long, six stamens almost equal in length—three with anthers 2.5-3 mm long, three with 3-5 mm anthers—arranged more or less parallel to the open perianth parts. The differences were first recognised in live material sent from Brisbane through the courtesy of Dr. Blake and Mr. Coal-drake. The morphological differences were found to persist in cultivation. In an attempt to elucidate the relationship between these types artificial cross-pollinations between them have been attempted. The results to date show that both types are self fertile and that crossings in which the large flowered form is the female result in no seed production, whereas the reciprocal (small flowered female) sets seed. So far plants have not been raised from such experimental crosses.

During an extended collecting trip in 1959 I was able to examine several habitats for *T. tuberosus* near Brisbane. Plotting the occurrence of the two types gave a distribution in which the types replaced each other without obvious reason at intervals in a north-south direction (the sampling having been carried mostly along the Brisbane-Maryborough road which runs more or less north-south). The area is mostly occupied by "wallum"—coastal plain country on which grows *Banksia aemula* and *Melaleuca leucadendra* (sensu lato). There are slight altitudinal variations of the order of 100 feet, the lower parts tending to be water-logged. From the study of the distribution of the two types the pattern emerges that on the lower wetter parts the smaller flowered type is found and that with increase in elevation it is replaced by the larger flowered type. In an area of c. 300 × 10 yards at Beerburrum both forms were found in ratios varying from 8:0 (large:small) to 1:9 over the area. Again the higher proportion of the smaller flowered type was found on the lower parts. The sampling was obviously confined to the plants in flower at the time and does not represent a complete sample of the population. It demonstrates that the two types are distinct and are able to maintain their identities in a mixed population. It is proposed on the basis of the evidence presented to separate the types at the subspecific level, the large flowered one to be known as *T. tuberosus* subsp. *tuberosus* and the smaller flowered type as *T. tuberosus* subsp. *blakei*. In the same tuberous-rooted, paniculate inflorescenced group Robert Brown (1810) described *T. elatior*—a taller, more robust plant with

larger flowers collected from the north coast of Queensland and islands in the Gulf of Carpentaria. Similar plants have been found by me in inland New South Wales and although no experimental work has been done it is thought that the morphological variation does not merit specific rank and that until the results of investigations are known such plants should be included within the subspecies *tuberosus*.

By comparison with the distribution of *T. tuberosus* which shows a mainly north and south trend, the distribution of *T. patersonii* shows largely an east-west trend occurring as it does in southern New South Wales, Victoria, Tasmania, South Australia, southern Northern Territory and extra-tropical Western Australia. It is worth noting that on present knowledge it is the only widespread extra-tropical *Thysanotus* species recorded from eastern and western Australia, in addition it is the only species so far recorded from Tasmania, whence the type specimen was collected. Kunth in his *Enumeratio* (1861) delineated the species *T. manglesianus* based on a specimen collected from New Holland by Captain Mangles, in the course of the description mention is made that a specimen collected by Gaudichaud from the Vasse River (near Busselton, Western Australia) is identical with the type. Subsequent workers as for example Baker (1877) have submergered *T. manglesianus* within *T. patersonii*. One of the distinctions made by Kunth was the larger flower size in his specimens compared to Brown's type specimens from Tasmania. My researches have shown that in addition to larger flower size the anthers of the inner and outer whorls of stamens are dissimilar in size, whereas those in *T. patersonii* (sensu stricto) are nearly equal in length. An additional morphological character is the form of the ripe capsule which in the small flowered forms has an overall length of c. 5 mm and has the persistent perianth parts free at the tips whereas in the large flowered form the overall length is c. 13 mm of which c. 8 mm is made up of the persistent perianth parts closely appressed and slightly twisted together. The size of the capsule itself in the two forms is almost the same. The two forms are found growing in nearby localities in Western Australia, but so far no evidence has been obtained of the presence of intermediates. As mentioned above some species of *Thysanotus* possess anthers which dehisce by longitudinal slits, *T. patersonii* is one of these and as a result of the larger amounts of pollen shed it is less likely that cross-pollination between types would occur in this species. I therefore propose to re-establish *manglesianus* as an epithet at the subspecific level to describe the large flowered, western form of *T. patersonii*. The small flowered plant as exemplified by Brown's Tasmanian collection becomes *T. patersonii* subsp. *patersonii*.

In *T. patersonii* it has also been possible to demonstrate the existence of polyploidy—the occurrence in plants of chromosome numbers greater than the typical diploid number which for *Thysanotus* is 22. A chromosome count of c. 80 was reported on Tasmanian material (Jackson, unpublished data) and subsequently in association with Jackson I was able to show

that this was 88—the plant would therefore be termed an octoploid. There is in this case no morphological difference from other plants of *T. patersonii*, we therefore have an example of a chromosome race whose identification is only possible from microscopic examination rather than from macroscopic examination—the latter the more normal technique in herbaria. So far no chromosome numbers intermediate between diploid and octoploid have been found, one would expect that—unless they had been lost in the evolutionary process—there would be tetraploid types in existence. Live plants have been obtained from various localities in Tasmania and northward on the mainland towards Newcastle, N.S.W.—which seems from herbarium records to be the northernmost limit for the species in eastern Australia. Cytological investigation of these plants may, it is hoped, provide evidence of the existence of the tetraploid race. A similar situation of chromosome polymorphism without morphological differentiation has been found by James (unpublished data) working on Western Australian populations of *Isoloma*.

Hagerup (1932) stated that in the Northern Hemisphere more northerly populations possess a higher proportion of polyploids. Subsequent workers who analysed the Spitsbergen flora were however not able to substantiate this point. Manton (1937) working on a crucifer *Biscutella laevigata* which had been found to possess diploid and tetraploid races in Europe, showed that the distribution pattern was such that the tetraploid occupied the areas which had most recently been freed from ice and that the diploid remained in the lower altitudes. This was held to show that the more recently evolved tetraploid possessed the ability of more rapidly colonising new habitats. Other workers have subsequently found evidence from other plants which agrees with this interpretation. It may well be that in the case of *T. patersonii* an ancestral diploid (or possibly tetraploid) form migrated across the then existing Bass Isthmus and that under glacial conditions in Tasmania these forms were replaced by higher polyploid forms and themselves failed to survive. That the octoploid is not recent in origin is suggested by the regularity of its meiotic division and the possession of high fertility. It would seem that the process of "diploidisation" had gone on with the production of regular meiosis and the restoration of fertility. The possible alternative would be that another species of *Thysanotus* was able to hybridise with the ancestral form and that from a putative sterile hybrid the present octoploid was developed by chromosomal doubling. The possible objection to this latter theory would be that some trace might be expected of introgression (Anderson 1949) of characters from the other parent and one would expect a difference in morphology between the octoploid and its mainland relatives. This has not so far been observed.

The last example I wish to quote from *Thysanotus* is the case of the two species *T. triandrus* and *T. multiflorus*. They are both solely Western Australian in distribution and both belong to the section of the genus possessing only three stamens. They are similar in

habit, they have fibrous, non-tuberous rooted stocks surrounded by leaf bases both current and past, the leaves are without petioles and erect. The scape is simple and has a single terminal umbel of flowers. The distinguishing characters of the two species are *T. triandrus*—leaves linear-lanceolate, channelled, covered with a more or less dense tomentum; *T. multiflorus*—leaves linear, flat, glabrous. In the latter species luxuriant specimens may develop a second sessile or shortly stalked inflorescence some distance below the terminal one. Experimental cross-pollination between the species produced seed and subsequently a mature plant. The hybrid is somewhat intermediate between the parents: it has the flat linear leaves of *multiflorus* which develop a tomentum similar to that of *triandrus*. Only a single plant reached maturity and rather than use the buds for cytological investigation, experimental self- and back-cross pollinations were carried out. No seed was obtained from either of these experimental crossings. From results so far one can tentatively conclude that in spite of the production of a viable hybrid plant there is either insufficient homology in the two chromosome sets or that breakdown occurs in the development of endosperm, leading to the failure to produce viable seed. If this is the true picture it means that should intercrossing take place in the field the production of hybrid individuals does not automatically mean the production of hybrid swarms and the subsequent possible breakdown of the species boundaries. Such an intercrossing is not very likely under natural conditions since the parents are ecologically isolated—*T. triandrus* is found on the sandy soils of the coastal plain and the inland sand plain, whereas *T. multiflorus* is distributed through the eucalypt forest on the lateritic soils of the Darling Range. There are areas in south-west Western Australia where *T. multiflorus* tends to occur on sandy soils but in these areas *T. triandrus* is absent. If future experimental self-pollination of hybrids between the two species results in the production of mature seed and subsequently plants, one would then be justified in reducing the two parental species to the status of sub-species of a single species, since the possibility of their being able to exchange genes would have been demonstrated.

A second case of polyploidy has been found in the genus—within *T. multiflorus*, here at the tetraploid level $2n = 44$. Two localities are known for plants which on morphological grounds would be referred to *T. multiflorus*, but which occur on the coastal plain associated with swampy conditions, one near Welshpool and the other near Pearce. In each locality *T. triandrus* occurs in the vicinity. The tetraploid plants are fertile and possess a regular meiotic division. Taking the cytological and morphological evidence together it could be postulated that polyploidy here is a case of amphidiploidy—the doubling of the chromosome number in a sterile diploid hybrid, possibly similar to the one between *T. triandrus* and *T. multiflorus* to which reference has already been made. So far attempts to obtain seed from experimental crosses between the tetraploid and its putative parents have been unsuccessful. Another line

of attack is the possibility of artificially doubling the chromosome number of the experimentally produced hybrid and then checking the product against the naturally occurring $2n = 44$ plant. This would be a similar method to that used by Müntzing (1930) who was able to synthesise from the two diploid species of *Galeopsis* an amphidiploid which agreed very closely with the naturally occurring *G. tetrahit* whose origin had been hypothetically attributed to a cross between the ancestors of the two diploid species used in the experimental cross. Under such experimental conditions one cannot expect exact duplication of the existing form because of the time lapse which occurs between the original and the experimental cross which allows of possible evolution in the parental genotypes.

The cytological situation as it affects the evolutionary pattern of the Angiosperms in Australia has been recently reviewed by Smith White (1959) who commences by considering separately the woody and non-woody types of plants with Australian and extra-Australian distributions. After study of the available chromosome numbers of hardwood genera of families such as Myrtaceae, Proteaceae, part of Rutaceae, Epacridaceae and Casuarinaceae he finds that within Australia there is marked diversity in chromosome numbers compared with extra-Australian members of these groups and that this diversity is at generic rather than specific level. At the species level polyploidy is rare and number variations are unknown within species.

In softwood or herbaceous types he finds it difficult to obtain groups of comparable size to those just mentioned, his choice is the families Goodeniaceae and Lobeliaceae and the genera *Danthonia* and *Nicotiana*. Within the two softwood families polyploidy is frequent, reaching levels of hexaploidy and octoploidy in the Goodeniaceae where many cases of intraspecific polyploid series are found. In the genus *Lobelia* different base numbers but no polyploidy are found in the Australian species, whereas extra-Australian species possess a single base number and show polyploidy both at intra- and interspecific levels. *Nicotiana* shows a similar situation to that pertaining in *Lobelia*, there is chromosome number diversity but little polyploidy in the Australian compared to the extra-Australian species. An entirely different situation holds in the grass genus *Danthonia* where, as shown by the data of Brock and Brown (1961) high polyploids up to decaploid level with $2n = 120$ are found in a series of species which are considered to be primitive as shown by the possession of hairs on the lemma (Table II). Associated with reduction in the number of hairs there is a corresponding rise in the proportion of diploid species and reduction in the maximum level of polyploidy to the hexaploid level.

The other monocotyledons mentioned by Smith White are the grass genus *Themeda* and the liliaceous genera *Sowerbaea* and *Blandfordia*. The two former genera differ markedly in number of species *Themeda* having many and *Sowerbaea* only two. They are similar in the possession of polyploidy, although its geographical occurrence is reversed in the two genera.

TABLE II

Polyploidy and evolutionary series in species of *Danthonia* (after Brock and Brown 1961)

Lemma hairs	2n = 24	2n = 48	2n = 72	2n = 96	2n = 120
S	<i>linkii</i>	<i>linkii</i> & var. <i>fulva</i>	<i>linkii</i> var. <i>fulva</i>	<i>induta</i>	<i>induta</i>
C	<i>longifolia</i>	<i>longifolia</i>	<i>induta</i>	<i>pallida</i>	6%
A	<i>carphoides</i>	<i>clelandii</i>	<i>pallida</i>	13%	
T	<i>semiannularis</i>	<i>geniculata</i>	19%		
E	<i>occidentalis</i>	<i>richardsonii</i>			
R	31%	31%			
E					
D					
T	<i>caespitosa</i>	<i>caespitosa</i>	<i>caespitosa</i>	<i>procera</i>	
W	<i>setacea</i>	<i>setacea</i>	<i>bipartita</i>	7%	
O	<i>acerosa</i>	var. <i>brevisetata</i>	<i>purpurascens</i>		
R	<i>alpicola</i>	<i>eriantha</i>	21%		
O	<i>auriculata</i>				
W	<i>duttoniana</i>				
S	<i>monticola</i>				
	50%				
R	<i>laevis</i>	<i>laevis</i>	<i>laevis</i>		
E	<i>pilosa</i> &	<i>pilosa</i> &			
D	var. <i>paleacea</i>	var. <i>paleacea</i>	11%		
U	<i>nivicola</i>				
C	<i>penicillata</i>				
E	<i>racemosa</i>				
D					
	66%				

In *Sowerbaea* the eastern species is tetraploid and the western diploid. *Themeda australis* according to the data of Hayman (1960) has a diploid distribution ranging from Tasmania to southern Queensland. In the same region there occurs a tetraploid, occasional triploids, pentaploids and three localities for a hexaploid. In the central, western and northern part of the continent the diploid is absent, the tetraploid is widely represented and a single locality for the hexaploid is reported.

The genus *Blandfordia* extends into Tasmania and it is reported that this species is tetraploid, whereas the three species in eastern New South Wales are diploid. This situation parallels to some extent that already reported above for *Thysanotus patersonii* and is the reverse of that reported in *Themeda australis* where only the diploid is found in Tasmania.

Smith White (1959) compared the chromosome numbers of the eastern and western Australian members of the families already mentioned under hardwood types above and found almost exact agreement between them (Table III). This fact he uses as the basis for a theory that the Angiosperms arose outside Australia and then migrated as an already differentiated body from the north. Let us look at the distributional and variational pattern in *Thysanotus* in the light of this theory. A single species is found in the Philippines, China, Siam, Malaya, New Guinea and also in tropical Australia. In New Guinea the presence of *T. tuberosus* is also reported. Of the two species with distributions outside Australia the one with the wider distribution, *T. chinensis*, is a plant with little or no adaptive morphology to life in drier conditions, it has thin mesophyllous leaves and a fibrous root system without tubers. This habit is shared with *T. triandrus*, *T. multiflorus*, *T. asper* and *T. glaucus*—all of which are western in distribution. *T. tuberosus* possesses a root system

with tubers and although the leaves are mesophyllous they die back and do not have to survive summer conditions. The other Australian species possess either a tuberous root system or an underground rhizome. Of these two types all those with tuberous roots possess aerial parts which die back and are replaced annually, whereas the rhizomatous forms have perennial above-ground parts which may be either leafy or somewhat rush-like.

If we accept Smith White's hypothesis it would require that *T. chinensis* would have been the original form developed outside Australia and that it was waiting—as he puts it—“at the bridgeheads” when migration began. It would seem unlikely that a form with tuberous roots and an annual cycle of leaf renewal would be evolved under tropical conditions in New Guinea; this statement being based on the adaptive value to dry conditions of the root system and also on the lack of the colonisation of the Malay Archipelago by *T. tuberosus*. On the other hand if we require that *T. tuberosus* or some ancestral form of this species evolved in Australia the time during which this could occur is limited by the necessity for a land connection for the northward migration to New Guinea. This theory of the origin of *Thysanotus* conflicts with the view recently expressed by Burbidge (1960, p. 194) that “it would appear that *Arthropodium* and *Thysanotus* may be Australian elements and that they should be recognised as such where they occur outside the region.”

If the distribution of the tribe Asphodelae (to which *Thysanotus* belongs) is plotted in terms of the areas occupied by its constituent genera the following pattern emerges—the two biggest genera *Anthericum* and *Chlorophytum* have a wide tropical and sub-tropical distribution, the next largest genera occur in South Africa and Central Asia, *Thysanotus* is fifth in order. If the geographical distribution is looked

at in terms of number of genera in a given area then the Australian continent with a total of eleven genera has the highest concentration, these are distributed as six occurring in both east and west, three in the east only and two occurring only in the west. South Africa has only four genera, although one of these is the large genus *Bulbine*. Only a few of the genera within the Asphodelae which are represented in Australia are also found beyond it; for example *Arthropodium* is found in New Zealand and New Caledonia, *Herpolirion* in New Zealand, *Chlorophytum* generally distributed in the tropics and *Caesia* in South Africa. If the genera with Australian distributions are plotted on a basis of rough known localities it is found that the largest number of species occur in the south-east and south-west of the continent. If one invokes Willis' Age and Area hypothesis (Willis 1949) the evidence from geographical distribution just presented favours a southern rather than a northern origin for the group.

TABLE III

Comparison of basic chromosome numbers in hardwood genera of eastern and south-western Australia (after Smith White 1959).

Family and genus	Basic numbers	
	South-western	Eastern
Myrtaceae		
<i>Actinodium</i>	6	—
<i>Darwinia</i>	6, 9	6
<i>Homoranthus</i>	—	6, 9
<i>Verticordia</i>	6, 8, 9, 11	—
Boroniaceae		
<i>Zieria</i>	—	18
<i>Boronia</i>		
<i>valvatae</i>	16	16
<i>terminales</i>	9	9
<i>pinnatae</i>	11	11
<i>Eriostemon</i>	14	14
<i>Phebalium</i>	16	16
Proteaceae		
<i>Persoonia</i>	7	7
<i>Grevillea</i>	10	10
<i>Hakea</i>	10	10
<i>Conospermum</i>	11	11
<i>Isopogon</i>	13	13
<i>Petrophila</i>	?	13
<i>Adenanthos</i>	13	—
<i>Lambertia</i>	14	14
<i>Banksia</i>	14	14
<i>Dryandra</i>	14	—
Epacridaceae		
<i>Styphelia</i>	4	4
<i>Asiroloma</i>	4	4, 7
<i>Gonostephium</i>	8	—
<i>Melichrus</i>	—	8
<i>Leucopogon</i> p.p.	4	4
<i>Leucopogon</i> p.p.	6	6
<i>Leucopogon</i> p.p.	11	11
<i>Brachyloma</i>	7?	9
<i>Acrotriche</i>	9	9
<i>Lissanthe</i>	—	7
<i>Monotoca</i>	—	12
<i>Andersonia</i>	12	—
<i>Sprengelia</i>	—	12
<i>Lysinema</i>	12	—
<i>Epacris</i>	—	13
<i>Woolisia</i>	—	13
<i>Richea</i>	—	13
<i>Dracophyllum</i>	—	13
<i>Sphenotoma</i>	6, 7	—
Casuarinaceae		
<i>C. glauca</i> group	9	9
<i>C. distyla</i> complex	11	11

If we look at the Australian distribution of *Thysanotus* species we find that in common with such genera as *Banksia* and *Hakea* the genus is predominantly western, twenty-six species being found in south-west Western Australia compared to five in south-eastern Australia. The section *triandrae* with the reduced number of three stamens is restricted to Western Australia. Of species which occur in both east and west mention has already been made of *T. patersonii* and *T. chinensis*, in addition *T. tenellus* although mainly western is found in South Australia. There are however examples of what may on further investigation prove to be vicarious species pairs as, for example *T. tuberosus* and *T. thyrsoideus*: *T. juncifolius* and *T. pseudojunceus*.

Evidence for a much wider distribution of *Thysanotus*, at least in Western Australia is provided by the occasional occurrence of very disjunct populations of the two species *T. dichotomus* and *T. sparteus*. Both species are normally restricted to the *Eucalyptus marginata*-*E. calophylla* forest (the Jarrah forest) of the Darling Scarp. *T. sparteus* has a slightly wider distribution and is also found on the coastal plain with *E. gomphocephala* (Tuart) and *Banksia menziesii*. Isolated occurrences of these *Thysanotus* species are found associated with granitic outcrops in what is now the Western Australian wheat belt. None of these localities has specimens of *E. marginata* and curiously the one locality (Jilakin Rock) with Jarrah has not so far been found to contain *Thysanotus*. Gardner (1944) in "The Vegetation of Western Australia" makes a special category of plants associated with the habitat provided in the vicinity of these outcrops, which provide a higher level of soil moisture as a result of the runoff from the rocks.

If we attempt to reconstruct the history of *Thysanotus* we could—following Smith White—postulate an invasion from the north by *T. chinensis* which did not go very far south in eastern Australia but reached further in Western Australia; secondly the evolution of tuberous rooted forms either simultaneously in east and west or at a single locality followed by migration; thirdly migration of a tuberous rooted form to New Guinea; fourthly the development of plants with rhizomatous rootstocks and the lack of formation of root tubers (this again needs two centres of origin or migration from a single centre); fifthly the development of climbing forms and the migration of these to Tasmania—the absence of other species from Tasmania requires either a limitation of southward migration or the complete destruction of immigrants during the period postulated above for the production of the Tasmanian polyploid *T. patersonii*; sixthly the evolution of the three stamened species in Western Australia followed by; seventhly further speciation in Western Australia to account for the larger number of species in that region. Future work on relationships of somewhat similar—morphologically speaking—eastern and western species may help to decide between the alternatives given in the second and fourth stages, further work with

populations of *T. patersonii* should help solve the problems mentioned under the fifth heading.

In summary then we may say that a study of variation in *Thysanotus* provides evidence of variation at single gene mutation level (flower colour); the occurrence of intraspecific polyploidy (*T. patersonii*); the occurrence of subspecific variation maintained by partial genetic barriers and by the pollination mechanism (*T. tuberosus* and *T. patersonii*); the presence of ecologically isolated species which have diverged to the extent of being able to produce sterile hybrid progeny, with which is associated the possible production of an amphidiploid (*T. triandrus* and *T. multiflorus*) and also the presence of ecotypes in clinal form (*T. triandrus* and *T. multiflorus*).

A postulated pattern of invasion and speciation is suggested based on Smith White's hypothesis, posing however the question as to the possibility of a migration at a later date of one species in the reverse direction. Much work still remains to be done on this and many other similar and related problems before the picture of the evolution of the Australian flora will be in any way complete.

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2.—The Largest Known Australite and Three Smaller Specimens from Warralakin, Western Australia

By George Baker*

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A large oval australite core recently discovered near Warralakin, Western Australia, is incomplete because of artificial fracturing and relatively severe natural weathering but it is nevertheless the largest australite so far brought to the notice of the scientific world. Even with the fracture fragments missing, the specimen weighs 20 grams more than the heaviest australite recorded to date. It weighs 238 grams; its weight at the time of landing upon the earth's surface has been estimated as approximately 230 grams. Reconstruction of the approximate primary shape of this australite reveals that about 35 per cent. of its original bulk was lost by ablation from aerodynamic friction during passage through the earth's atmosphere at high velocities.

Three smaller australites subsequently found in the same general area, six to nine miles south of the Warralakin-Warrachuppin railway line, are briefly described.

Introduction

The largest australite so far discovered was unearthed during post-hole digging operations which penetrated to a depth of 20 inches in soil, approximately 16 chains north of the south-west corner of Block 301, 9.6 miles S.S.E. of Warralakin Siding, Yilgarn Area, Western Australia (Fig. 1). The geographical position of this locality is $31^{\circ} 08' 25''$ S. and $118^{\circ} 41' 21''$ E. The specimen was found in August, 1957—previously to which no other australites had been observed in this area.

Warralakin is 175 miles E.N.E. of Perth, Western Australia, and is on the Wyalkatchem-Southern Cross railway loop-line.

The specimen was recovered in a slightly chipped and weathered condition by Messrs. D. S. and A. V. Poole on the property "Coppin Rock" near Warralakin. The slight chipping resulted from damage by the post-hole digger. Screening of the soil from the post-hole failed to recover the detached fragments. Unfortunately a large piece was subsequently fractured from the end of the specimen with a cold chisel and lost. Even without this fragment, however, the specimen constitutes the largest australite known to science. In the unbroken condition it would have been approximately 50 grams heavier than the previously recorded (Fenner 1955) heaviest australite.

This australite is lodged in the geological collection (Reg. No. 8925) of the School of Mines of Western Australia, Kalgoorlie, to

which institution it was donated by Mr. R. W. Poole (of Gold Mines of Kalgoorlie), a brother of the discoverers.

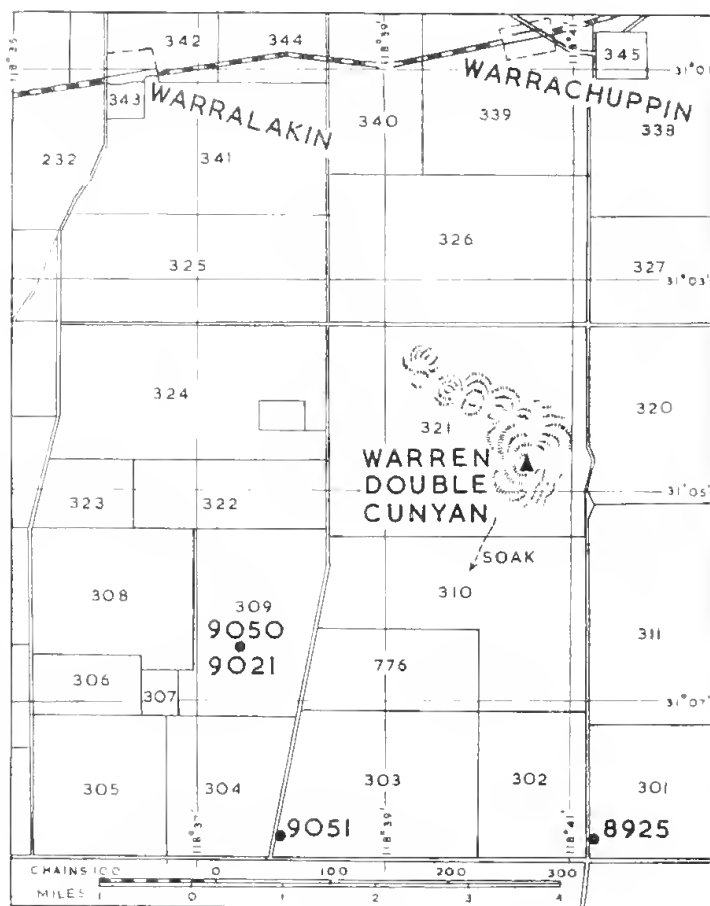


Fig. 1.—Locality map of the area south of the Warralakin-Warrachuppin railway line, Yilgarn Area, Western Australia, showing sites (full circles) of recently discovered australites. The large figures are the registered numbers of the australites in the geological collection of the School of Mines of Western Australia, Kalgoorlie.

The precise depth and orientation of the specimen in the soil could not be noted at the time of discovery, but detailed inspection of all surfaces and of the clay lodged in pits on them leads to the conclusion that the posterior surface lay downwards in the soil. The clay on the posterior surface was redder in colour due to more ironstaining, whilst that on the anterior surface was biscuit-coloured to almost white due to leaching, and the redder coloured clay on the posterior surface was rather more firmly cemented into pits and narrow flow lines. In

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the vicinity of the find, the area is relatively well-timbered, the surface is sandy with a few pebbles brought up by the roots of fallen trees.

The soil in which the specimen was found is of the "sand plain" type. In Western Australia, this is often a leached "A" horizon but, irrespective of the initial origin of the sand, it has usually been wind-drifted to a greater or lesser extent. It can be quite confidently stated that this large australite occurred at shallow depth in wind-blown sandy soil.

The deduced position of rest of the australite, i.e., with its anterior surface upwards, is the reverse to its position of aerodynamically stable orientation during earthward flight. Nevertheless this is the stable position of rest on the earth's surface, just as for the majority of australites exposed on the surface for which this position was observed on discovery. The stable position of rest was either attained immediately after striking the ground, or resulted subsequently when specimens were moved by transporting agents after landing.

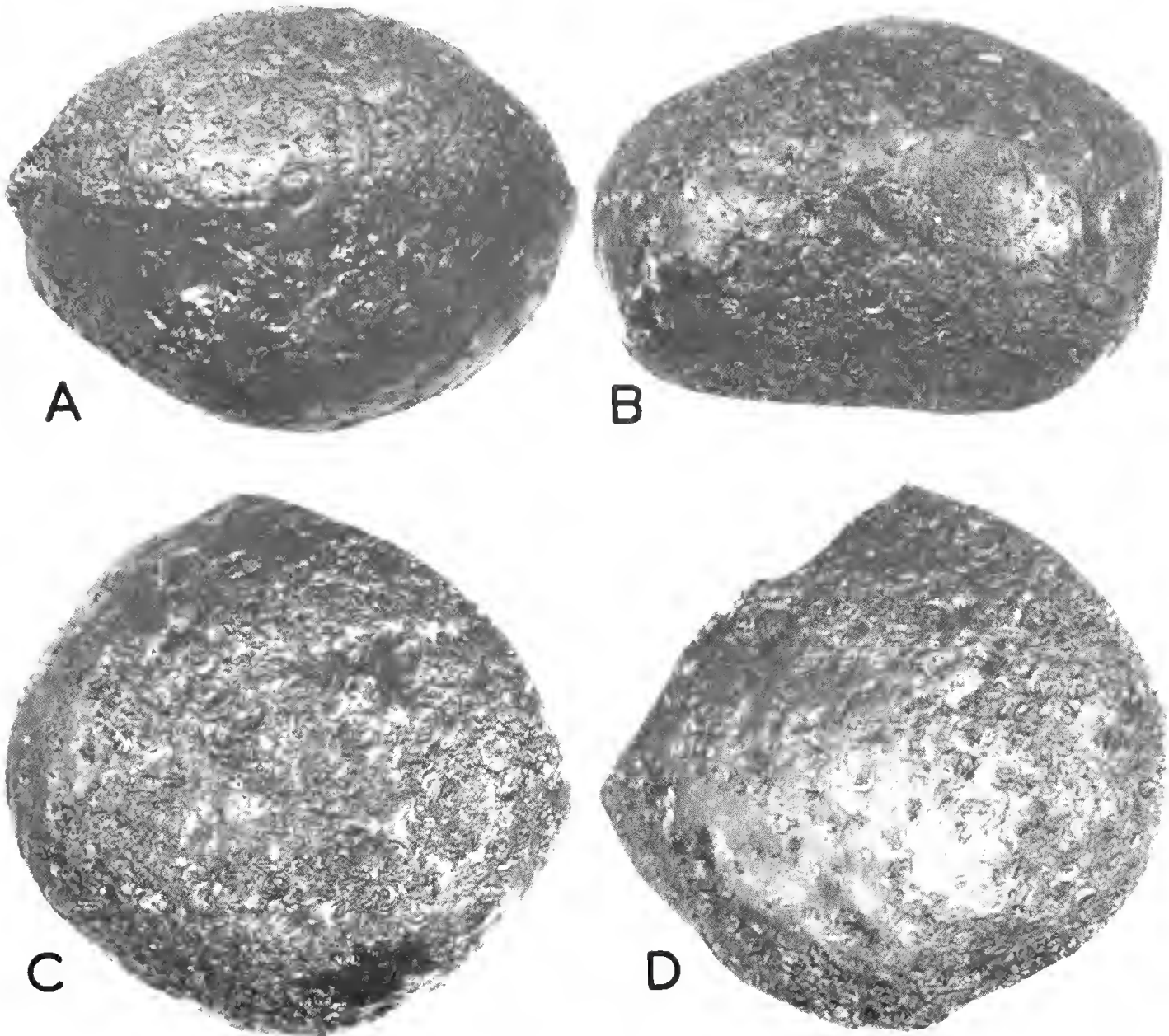


PLATE I

The largest known australite (Reg. 8925, geological collection, School of Mines of Western Australia, Kalgoorlie). From south-west corner of Block 301, 9.6 miles S.S.E. of Warralakin Siding, Western Australia.

Figs. A to D—showing etched "bruise-marks", a few of which resemble "höfchen" and "tischchen", on an oval australite core. A = end-on view across shortest diameter; posterior surface uppermost; rim poorly preserved ($\times 1.16$). B = side view across largest diameter; posterior surface uppermost; equatorial zone at right-hand end relatively well preserved ($\times 1.10$). C = anterior surface ($\times 1.10$). D = posterior surface ($\times 1.10$).

(Photographs by K. L. Williams.)

Description of Specimen

As submitted for examination, the weathered specimen revealed a small quantity of light buff-coloured to reddish-brown lateritic sandy soil partially cemented and partly jammed into shallow pits and lunate to circular shallow grooves on all surfaces, except the newly exposed (artificially fractured) surface. It was necessary to remove all secondary material prior to determining the specific gravity of the australite.

The weathered surface has a dull lustre and reveals occasional poorly pronounced "höfchen" and "tischchen" structures brought out by differential solution-etching by soil solutions. Rare, fine flow lines occur on parts of the surface, while only a few straight, slightly deeper grooves with parallel walls are present in one place. Many of the markings on the posterior and anterior surfaces of the specimen resemble chatter-marks brought about by collisional bruising, but since the australite was found in a milieu where natural agencies likely to have caused these features are apparently wanting, the possibility arises that the marks may have been due to aboriginal activities (e.g. use as a pounding stone, etc.), although this is difficult to prove.

The broken surface reveals the highly vitreous lustre and conchoidal fracture with subsidiary ripple fracture pattern that is so characteristic of freshly fractured tektite glass. Up to three dozen minute internal bubbles can be detected on the fractured surface with the aid of a 10× hand lens. The area of the fractured surface is approximately 12.5 cm², and if the internal bubbles are maintained in this distribution throughout the interior of the large australite, they could partly account for the specific gravity of the tektite glass as a whole being lower than usual for australites from the western portions of the Australian tektite strewnfield. These bubbles are more or less spherical in shape, and range from 0.25 mm to nearly 0.75 mm in diameter.

A rim (cf. Baker 1959, p. 39) is just discernible around most of the periphery of the specimen (see Plate I, Figs. A and B), and is sufficiently pronounced to aid in discriminating between the anterior and posterior surfaces of the australite.

The tektite glass is jet black and opaque in reflected light for the specimen in bulk, but yellowish bottle-green and translucent in transmitted light on the thinner edges of the fractured surface and in small splinters detached for refractive index determinations.

Dimensions, Weight and Specific Gravity

The specimen is 42 mm in depth (= thickness) and 62.5 mm in width as determined from the non-fractured portions of the australite. Its present length is 65 mm, but the original length (on reconstruction of the fractured form) was approximately 70 to 72 mm. It is thus an oval australite core. It weighs 238.00 grams and has a specific gravity value of 2.409 as determined in distilled water (T_{H₂O} = 12.8° C.) on a Mettler K-type balance. The specific gravity is approximately that of

the mean specific gravity value determined for 1,086 specimens of australites (Baker and Forster 1943, p. 403), but is significantly lower than the general run of specific gravity values for australites from the western half of Australia, evidently because of its content of small bubbles.

The volume of the cleaned specimen is 98.8 cm³. Reconstruction of the unbroken (but weathered) form reveals that approximately one ninth was removed by artificial fracturing, so that the specimen as found would have weighed about 265 grams. It has not been possible to reconstruct the specimen accurately enough to ascertain its size as it would have been on first landing upon the earth's surface from an extra-terrestrial source, but an approximate estimate of the amount weathered from this large oval australite core indicates that in the perfectly preserved state, the original weight would have been in the vicinity of 280 grams.

Australites weighing over 200 grams are extremely rare, and only two others are known. One, weighing 218 grams, was found at Lake Yealering, Western Australia (Fenner 1955), the geographical position of which is approximately 32° S. and 118° E., the other came from Karoonda, South Australia (Fenner 1955), at 35° S. and 140° E. and it weighs 208.9 grams. The Lake Yealering specimen is lodged in the collection of the Western Australian Museum in Perth, Western Australia, and the Karoonda specimen is in the South Australian Museum collection in Adelaide, South Australia.

Only eleven specimens are known that weigh over 100 grams and under 200 grams. Seven of these are recorded by Fenner (1955, pp. 90-91); the other four are:—a boat-shaped form of 141.63 grams weight from Port Campbell, Victoria (Reg. No. 11402, National Museum of Victoria collection), a round core of 135.16 grams weight from Gymbower near Goroke, Western District of Victoria (National Museum of Victoria collection), a round core of 111.25 grams weight from Lake Wallace near Edenhope, Victoria (Reg. No. E1986, National Museum of Victoria collection), and a boat-shaped form of 107.46 grams weight from near Narembeen, Western Australia (Reg. No. 8950, geological collection, School of Mines of Western Australia, Kalgoorlie).

Refractive Index and Estimated Silica Content

The refractive index of the glass varies according to the chemical composition of different internal schlieren, but does not show a wide range in the small fragments examined. Values obtained by the Immersion Method using monochromatic (Na) light and employing microscopic fragments removed from the freshly fractured surface of the specimen by light pressure flaking, showed a range from:—

$$n_{Na} = 1.504 \text{ to } n_{Na} = 1.506$$

The specific refractivity (k) of the glass, determined from the relationship $k = n - 1/d$ (where n = the refractive index, and d = the specific gravity of the specimen), ranges from 0.2092 to 0.2100, according to the composition of the different schlieren.

From the Silica-Specific Gravity and the Silica-Refractive Index graphs for tektites generally (see Barnes 1940; Baker 1959), the silica content of the specimen is estimated to be approximately 74 per cent. In view of the possibility that the content of small internal bubbles lowers the specific gravity of this specimen, however, both the silica content and the specific refractivity may be slightly different from the estimated values, but the silica content is likely to be no more than one or two per cent. lower.

Curvature of Surfaces

Silhouette traces of the weathered specimen reveal that arcs of curvature across the shortest diameter of the australite are:

$$R_B = 34.5 \text{ mm. and } R_F = 31.5 \text{ mm.}$$

where R_B = the radius of curvature of the posterior (back) surface and R_F = the radius of curvature of the anterior (front) surface. Across the longer diameter, the radii of curvature are $R_B = 40.9$ mm and $R_F = 44.1$ mm, but constructed circles do not fit as accurately to the arcs of curvature in this direction as to the surface curvature across the shorter diameter.

The original form, prior to modification by (i) ablation arising from aerodynamic friction during atmospheric flight, (ii) weathering by subaerial agents, and (iii) artificial fracturing after the specimen was collected, is estimated to have been an ellipsoid of revolution measuring approximately 7 cms \times 7 cms \times 8 cms in size. The depth of ablation in the stagnation point region (i.e. at the front pole of the specimen as aligned in aerodynamically stable orientation) was approximately 2.4 cms, and the overall amount ablated from the surface projected in the line of flight (i.e. the anterior surface) totalled about 60 cm³ in volume. Some 35 per cent. of the original form was thus lost during transit at ultrasupersonic speeds through the earth's atmosphere, by the processes arising from aerodynamic friction. This is a relatively low percentage loss compared with many smaller australites for which the range in amount of glass removed by ablation and fusion stripping plus flange shedding is from 32 per cent. to 98 per cent., with an average loss (for 65 specimens) of 50.5 per cent. (cf. Baker 1961a, Tables 4, 9 and 11). It is also much lower than the percentage loss range (61 to 96 per cent.) by ablation of ten larger, well-preserved australite cores from Port Campbell, Victoria (cf. Baker 1961a, Table 13).

Smaller Australites

Of the three smaller australites subsequently found some three and a half miles west and four and a half miles north-west of the site of the largest australite, two are boat-shaped and one oval-shaped. They and the largest australite were recovered from within an area of approximately nine square miles (Fig. 1).

Boat-shaped Form

The largest of the three smaller forms was found late in 1958 by Mr. D. S. Poole on Block 309 on H. M. Poole's property "Devon." This

is 7.2 miles east of south from Warralakin Sid-ing, or 31° 06' 36" S. and 118° 38' 34" E. Here the surface consists of residual gravel resulting from partial exposure of the laterite horizon.

The specimen was presented by Messrs. D. S. and R. H. Poole to the School of Mines of Western Australia, Kalgoorlie (Reg. No. 9021). Its dimensions are 38.5 mm long, 27.5 mm wide, and 16.5 mm deep (thick). It weighs 22.227 grams, and its specific gravity as determined in distilled water ($T_{H_2O} = 13^\circ \text{ C.}$) on a chemical balance is 2.425.

The specimen reveals a fairly well-defined rim separating the pitted and flow-lined posterior surface from the finely etch-pitted anterior surface. All structures on the australite, however, have been considerably modified by solution-etching, although the specimen is generally rather better preserved than the large australite described above. The boat-shaped outline of the specimen from front and back aspects is somewhat irregular (Plate II, Figs. A and B) due to erosion.

Portions of the flow-swirled central region of the posterior surface (Plate II, Fig. B) have been partly accentuated but some areas have been partly destroyed by solution-etching. Its general characteristics, however, are similar to the primary flow swirls on the posterior surfaces of better preserved australites.

In side- and end-on aspects, the outline is approximately that of a biconvex lens which has one diameter greater than the diameter at right angles. The radii of curvature across the shorter diameter (width) are $R_B = 16.8$ mm and $R_F = 17.2$ mm, with the arcs of curvature fitting those of constructed circles with these radii. The radii of curvature along the larger diameter (length) are approximately $R_B = 32.9$ mm, and $R_F = 25.9$ mm, but these two arcs of curvature do not conform accurately to the arcs of curvature of constructed circles with these radii, being rather flatter in the polar regions and steeper towards the rim of the specimen.

Oval Core

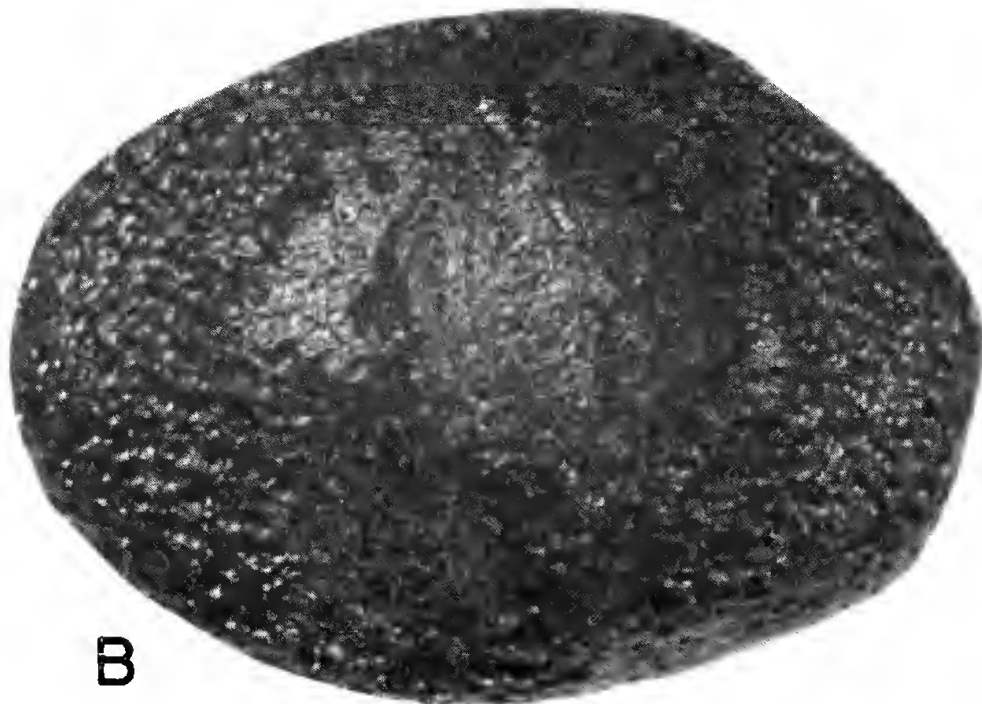
An croded oval australite core was found by Mr. A. T. Miles with its anterior surface upwards on 9th October, 1960. It was exposed on the gravelly surface of an area that slopes gently northward near the site of Reg. No. 9021 (Fig. 1). The specimen is now in the collection of the School of Mines of Western Australia, Kalgoorlie (Reg. No. 9050).

It weighs 7.102 grams and its specific gravity is 2.431 ($T_{H_2O} = 15.5^\circ \text{ C.}$). The longer diameter measures 22 mm, the shorter 18 mm and the depth (thickness) is 14 mm.

All surfaces reveal the effects of solution-etching and the sculpture pattern consists principally of small pits 0.2 mm across, ranging up to a few larger pits 3.0 mm across, mostly on the posterior surface. The larger pits reveal a few smaller pits and etched out flow lines on their walls. Where the larger pits are crowded together, sharp ridges separate one pit from its neighbour, and these parts of the surface resemble that of hammered metal.



A



B

PLATE II

A boat-shaped australite found $4\frac{1}{2}$ miles south-east of the large oval australite core shown in Plate I (Reg. No. 9021, geological collection, School of Mines of Western Australia, Kalgoorlie).

A = anterior surface showing fine etch pitting ($\times 2.57$). B = posterior surface with weathered and etched flow swirl surrounded by bubble pits modified by etching ($\times 2.57$).

(Photographs by K. L. Williams.)

A flaked equatorial zone is detectible but rather poorly preserved. It shows a few complexly contorted flow lines that have been exposed and accentuated by solution-etching. These are the surface expressions of an internal schlieren structure brought into prominence on the level to which weathering has advanced. Flaking around the equatorial zone has resulted in the specimen appearing like a conical core in side aspect.

Smaller Boat-shaped Form

Like all the other specimens from this area, the smaller boat-shaped form reveals no evidence that would indicate the former existence of a circumferential flange. If ever present, the flange has been completely removed, either by shedding during flight, or subsequently by subaerial erosion, and erosion has further modified the equatorial region and the posterior and anterior surfaces of the specimen.

It was found with the anterior surface facing upwards by Mr. D. S. Poole on 10th October, 1960, on the roadside between Block 303 and Block 304, approximately 22 chains from the south-west corner of Block 303 (Fig. 1.). Its registered number is 9051 in the collection of the School of Mines of Western Australia, Kalgoorlie, and it was discovered on top of the ground in gravel country similar to that on which Reg. Nos. 9021 and 9050 were found. The geographical location of the specimen is approximately 31° 08' 21" S. and 118° 37' 58" E.

Its weight is 5.9115 grams and its specific gravity is 2.433 ($T_{H_2O} = 15.5^\circ C.$). The measurements of the specimen are 26 mm long, 17 mm wide and 10 mm deep.

An old fracture surface at one end of the specimen is as prominently sculptured by weathering (mainly solution-etching) as are the posterior and anterior surfaces.

The rim separating the posterior from the anterior surface is detectible in places around the periphery of the specimen. Both surfaces reveal flow lines which represent the "outcrops" of an internal schlieren pattern that trends generally parallel with the outline of the form. Some of the smaller pits on both surfaces are evidently etch pits resulting from weathering, but several deeper rounded pits 1 mm across and elongated pits 2×1 mm in size are either overdeepened, originally superficial bubble pits or else internal bubbles exposed during the process of weathering.

Summary and Conclusions

The four australites recovered from the area south of the Warralakin-Warrachuppin railway line in Western Australia have all been modified by subaerial erosion to such an extent that their volumes on first landing on the earth's surface cannot be accurately determined. Their sculpture patterns are largely a result of weathering, more particularly by the process of solution-etching in sandy soils.

In borrow pits and the banks of dams in the district, the soil profile shows a variable thickness of sandy soil passing downward into a zone of discrete laterite nodules, and thence, in a depth of a foot or so, into compact laterite. The variable thickness of the sandy soil is partly attributable to wind, and, in some places, partly to rainwash. The largest specimen (Reg. No. 8925) was found where the wind-drifted sand is thicker than usual, and at this locality the 20" deep postholes barely entered the nodular laterite zone. This specimen could well have been exposed at one time and reburied under drifted sand. By contrast, two of the smaller specimens (Reg Nos. 9021 and 9050) that were found within four chains of each other, occurred right at the surface (gibber-plain type) in an area where partial stripping of the finer soil constituents had exposed nodules of laterite, among which the two australites were exposed to view. The fourth specimen (Reg. No. 9051) occurred on a gravelly, similarly stripped area. On gravelly slopes in this area, more thorough soil stripping down to the duricrust surface could readily result in removal of both lateritic nodules and australites and their transportation to flat-lying areas where re-burial in sandy soil is not improbable.

There is little doubt that these australites are post-laterite in age and their recovery from the overlying soils points to their recent age on earth (cf. Baker 1961b). Their surface sculpture is largely a result of weathering, whereby subaerial agents have reduced the sizes of the original specimens and developed structures that are a manifestation of their usually complex internal streakiness.

Acknowledgments

The author is indebted to W. H. Cleverly, B.A., B.Sc., head of the Geology Department, School of Mines of Western Australia, Kalgoorlie, for kindly submitting the australites for examination, and for obtaining details of their mode of occurrence and precise localities of discovery.

I am also grateful to Professor Rex T. Pridder for communicating the paper through his membership of the Royal Society of Western Australia.

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3.—The Flora of Granite Rocks of the Porongurup Range, South Western Australia

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The occurrence of the vascular and non-vascular flora on granite outcrops of the Porongurup Range in south Western Australia is described in relation to the environment. A systematic list of the algal, lichen, bryophyte, pteridophyte and angiosperm species of this flora is given.

Introduction

The Porongurup Range,† twelve miles east of the town of Mount Barker, consists of granitic rocks rising from the surrounding plain to a maximum altitude of 2,200 feet at the peak known as the Devil's Slide. Other peaks in the range include Castle Rock (altitude 1,870 feet), Twin Peak East (2,080 feet), Twin Peak West (2,040 feet), Gibraltar Rock (2,100 feet), Nancy's Peak (2,140 feet), Hayward Park Peak (2,000 feet), Angwin Park Peak (1,780 feet) and Collier Park Peak (2,080 feet).

The vegetation type of the range is an outlier of the Karri forest to the west. The trees include Karri, *Eucalyptus diversicolor*, the Marri, *E. calophylla* and to a less extent, *E. cornuta* and *E. megacarpa*. The under-storey of this forest includes the tall shrubs, *Trymalium spathulatum*, *Acacia pentadenia*, *Albizia distachya*, *Oxylobium lanceolatum*, *Mirbelia dilatata* and numerous species of smaller sclerophyllous shrubs.

This paper describes the flora of granite outcrops in this forest. Collections and observations were made at Castle Rock, Nancy's Peak, Devil's Slide, Gibraltar Rock and at several outcrops towards the base of the range.

One large slope about 80 feet above the Bolganup Dam (988 feet) has been called by the author, Rain Gauge Rock, after the automatic rain gauge set up on it since 1957 by the Hydraulics Branch of the Country Water Supply Department in connection with the Bolganup Dam.

Climatic Data

Rainfall

The existence of an automatic rain gauge at Rain Gauge Rock provides some evidence of the amount and monthly distribution of precipitation on the site of some of the lithophyllous communities described below. Table I

shows the annual rainfall for three consecutive years as taken from August, 1957, when the gauge was set up.

TABLE I

Annual rainfall for three consecutive years at Rain Gauge Rock (Bolganup Dam) Porongurup Range, Western Australia

Year	Rainfall in Inches
August, 1957-1958	20.16
August, 1958-1959	29.91
August, 1959-1960	52.03
Average Annual Rainfall	34.03

The average yearly rainfall for the nearby town of Mount Barker is 30.23 inches and that of Albany to the south of the Porongurups is 39.67 inches. A study of rainfall isohyets for this region indicates that the normal annual rainfall at the Porongurups could be about 34 inches, as both Mount Barker and the Porongurups are between the 30 inch and 40 inch isohyets, but much closer to the former.

An analysis of the monthly rainfall at Rain Gauge Rock into total winter and summer precipitation gives some idea of the seasonal desiccation to which the lithophyllous communities are subjected. In Table II the winter rainfall is taken as a six month period from May, when the winter rains start, to the end of October, and the summer rainfall as the precipitation from November to the end of April. The table shows that the lithophyllous communities are subjected to a wet half and a relatively dry half of the year. This evidence of summer desiccation supports the general climatic picture in the south-west of Western Australia where shallow-rooted plant communities are subjected to drought from about November to April.

TABLE II

Winter and summer rainfall at Rain Gauge Rock (Bolganup Dam), Porongurup Range, Western Australia

Winter rainfall in inches. May 1st-Oct. 31st	Summer rainfall in inches. Nov. 1st-April 30th
At Rain Gauge Rock	
22.59 (1958)	3.75 (1957-58)
23.56 (1959)	8.78 (1958-59)
27.05 (1960)	16.62 (1959-60)
Mt. Barker (Average)	
21.75	8.48

Temperature

The yearly average of daily maximum temperature for Mount Barker is 67.7° F, the monthly average of daily maximum temperature being greatest in February at 78.3° F. At Mount Barker the average of daily minimum

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† Although commonly written Porongurup, the name Porongurup was given by Surveyor-General J. S. Roe in 1835, and is followed by the Geographic Nomenclature Committee.

temperature is 48.3° F. the monthly average of minimum temperature being lowest in July at 42.0° F. These figures give some indication of the temperature extremes likely to obtain at the Porongurups, where unfortunately there is no recording station. The climatic data for Albany and Mount Barker were taken from Climatic Averages of Australia—Bureau of Meteorology, Melbourne, 1956.

Flora on the Granite Outcrops

The lithophyllous flora of granite rocks in south Western Australia is composed chiefly of bryophytes, lichens and sub-aerial algae. Small herbaceous vascular plants are also common in moss swards on granite slopes, while larger, perennial vascular plants are limited to the humus-filled crevices and depressions, or to the shallow soil at the border of outcrops.

The bryophytes and lichens of south Western Australia are reasonably well-known systematically from early collections made by visiting botanists, but there are few published records of these plants in relation to their habitats. Diels (1906), in his account of the vegetation of south Western Australia, did not describe the cryptogamic flora of rock outcrops. Likewise, Gardner (1942) described only the vascular flora in very general terms. Willis (1953), in his descriptions and analysis of the land flora of the Archipelago of the Recherche gave considerable ecological information on the lithophyllous flora of the igneous rocks of these islands. This flora shows some affinities with the lithophytes of the Porongurup Range, such as the wide occurrence in the Recherche of the mosses *Campylopus bicolor* and *Bryum billardieri*, and of the lichens, *Parmelia rutidota* and *P. conspersa*. The two floras differ strikingly, however, in the paucity of *Cladonia* species at the Recherche, whereas four species of this genus are common components of moss swards at the Porongurup Range. On the other hand the cushion plant, *Borya nitida* is common on granite slopes of the Recherche as it is on granite rocks of the Darling Range near Perth, but is conspicuous by its absence in the Porongurup Range.

Crustose Algal and Lichen Communities

The surfaces of granite tors and other steeply sloping outcrops which, to the casual observer, are bare rock surfaces, bear extensive communities of minute crustaceous lichens and blue green algae (Plate II, Fig. 2).

This type of community consists of the crustose lichen, *Caloplaca aurantiaca* and at least five other species of crustose lichens which to date it has not been possible to determine. The sub-aerial algae, *Calothrix* sp. and *Chroococcus* sp. occur in black, stain-like stands, mainly along seepage depressions over the outcrops.

The more conspicuous lichens, *Parmelia rutidota*, *P. imitatrix*, *P. conspersa*, *P. perlata* and *Sticta crocata*, also occur on steep rock faces whether exposed to full sunlight or partially shaded by the canopy of the Karri forest (Plate I, Fig. 1). *Sticta* appears to reach maximum vegetative development on gentle semi-shaded slopes where water seepage is high.

The moss, *Grimmia trichophylla*, is the only bryophyte found on the summits of granite tors and domes where it grows in small cushions in depressions and crevices resulting from weathering of the rock.

Moss Sward Communities

Low angled granite slopes throughout the Porongurup Range bear extensive moss swards which form mosaics with encrusting algal communities or crustose lichen communities (Plate I, Fig. 1 and Plate II, Fig. 1). Rarely is much of the rock surface devoid of plant life. Where recent exfoliation of the rock has occurred this is so, of course.

The association of species in these moss swards is variable but from examination and sampling of numerous slopes up to an angle of approximately 45° and of varying exposures to all points of the compass, but not shaded by trees or shrubs, the following species assessment may be given.

Two mosses, *Campylopus bicolor* and *Breutelia affinis* are the most extensive sward components. Other mosses in this sward include *Sematophyllum homomallum*, *Rhacocarpus humboldtii*, *Bryum argenteum*, *B. billardieri*, *Tortella calycina*, *Hedwigia imberbis*. The sward rarely exceeds three inches in depth where it overlies fairly smooth granite slopes and its surface is remarkably even considering the several moss components.

The high water-holding capacity of the mosses enables several herbs and geophytes to colonise the sward. The chief vascular plants are:—

Ophioglossum coriaceum
Triglochin centrocarpa
Aira caryophylla
Brizula muelleri
Centrolepis glabra
Pritzelia pygmaea
Bulbine semibarbata
Chamaescilla corymbosa
Tribonanthes variabilis
Hypoxis glabella
H. occidentalis
Pterostylis nana
Calandrinia pygmaea
C. calyptrata
Spergularia rubra
Drosera glanduligera
Crassula pedicellosa
C. macrantha
C. sieberiana
Trifolium dubium
Hydrocotyle callicarpa
H. diantha
H. blepharocarpa
Trachymene pilosa
T. anisocarpa
Homalosciadium verticillatum
Anagallis femina
Mitrasacme paradoxa
Erythraea australis
Bartsia latifolia
Styliidium calcaratum
S. corymbosum var. *proliferum*
Veronica calycinus
Polypompholyx tenella
Galium murale
Levenhookia dubia
Rutidosia multiflorus
Helipterum cotula
Angianthus tenellus
A. humifusus
Quinetia urvillei
Cenia turbinata
Hypochoeris glabra
Podolepis lessonii

1



2



PLATE I

Fig. 1.—Moss sward over granite with *Trachymene anisocarpa* in flower and *Pelargonium drummondii*. Granite surface in the background with *Parmelia rutidota*. The shrubbery in the right background consists of *Thryptomene saxicola* and *Stypandra grandiflora*.

Fig. 2.—Granite boulder with *Veronica calycina* in shaded recess. Right foreground with moss sward and *Villarsia calthifolia* in flower.

1



2



PLATE II

Fig. 1.—Moss sward on granite slopes with *Pelargonium drummondii*, *Cheilanthes tenuifolia* in centre and background, *Thryptomene saxicola* and *Stypandra grandiflora* shrubby towards edge of slope. *Eucalyptus diversicolor* and *E. calophylla* in the background.

Fig. 2.—Moss sward on granite slopes. Slopes and boulders with crustose lichens. *Pelargonium drummondii* amongst boulders. *Acacia* sp., *Lepidosperma effusum* and *Thryptomene saxicola* in background.

The lichen component of the sward includes the foliose forms, *Cladonia furcata*, *C. aggregata*, *C. chlorophaea*, *C. retipora*, *Siphula caesia*, *Sticta crocata* and *Collema* sp. These lichens grow embedded in the moss turf, but *Siphula* also grows in pure stands in exposed humus of shallow rock crevices. The only liverwort collected from the sward was *Fimbriaria conocephala*.

A few species of perennial vascular plants occur on granite slopes where either a crevice or the moss sward over depressions provides sufficient depth of humus for their root systems (Plate I, Fig. 1 and Plate II, Figs. 1 and 2). The fern, *Cheilanthes tenuifolia* occurs in extensive stands in the deeper parts of the moss swards. *Stypandra grandiflora*, *Pelargonium drummondii*, *Carpobrotus aequilaterus*, *Geranium pilosum*, *Lepidosperma effusum*, *Thryptomene saxicola*, *Darwinia citriodora* and *Agonis juniperina* are conspicuous perennials of the shrubbery of these crevices and depressions.

Communities of Shaded Crevices

Along the ridge of the Porongurup Range the exposed granite core of the range forms a massive system of tors with numerous deep crevasses and shallow caverns or recesses resulting from the sphaeroidal weathering of the granite. In these dissections, leaf litter and the products of exfoliation accumulate to form a shallow loam. Wherever this loam is sufficiently shaded by the adjacent rock a distinctive microflora develops (Plate I, Fig. 2).

The principal bryophyte and lichen elements of this microflora are *Lophocolea heterophylloides* and *Lepidozia parvistipa*, both of which form extensive mats over either loam or granite substrates. *Frullania latogaleata* is common in drainage depressions of the overhanging rock. *Sematophyllum homomallum* forms extensive mats. *Sticta crocata* is most common in shaded exfoliation depressions. *Marchantia cephaloscypha* is a rare but striking liverwort on humus of shaded undercuts.

Commonly associated with these bryophytes and lichens in the recesses of rock dissections are the ferns, *Asplenium flabellifolium*, *Adiantum aethiopicum* and *Anogramma leptophyllum*, the latter invariably accompanied by large numbers of its long-lived prothalli. *Asplenium praemorsum* occurs in more exposed crevices, although this fern is not common in the Porongurup Range.

The most common angiosperms in this habitat are *Corybas dilatatus*, *Cryptostylis ovata*, *Poa caespitosa*, *Pelargonium drummondii*, *Oxalis corniculata*, *Hydrocotyle hirta*, *Villarsia calthifolia* (a handsome species endemic to the Porongurup Range) and *Veronica calycina* (Plate I, Fig. 2). In rock dissections of more open aspect the following shrubs are common:—*Thryptomene saxicola*, *Sollya fusiformis*, *Stypandra grandiflora* and *Solanum nigrum*.

Systematic List of the Flora on Granite Outcrops of the Porongurup Range

Specimens of the following species are preserved in the Herbarium of the Botany Department of the University of Western Australia.

Algae

- Chroococcaceae
Chroococcus sp.
- Rivulariaceae
Calothrix sp.

Bryophyta-Hepaticae

- Lepidoziaceae
Lepidozia parvistipa Tayl.
- Harpanthaceae
Lophocolea heterophylloides Nees
- Frullaniaceae
Frullania latogaleata Herz.
- Marchantiaceae
Marchantia cephaloscypha Steph.
- Operculatae
Fimbriaria conocephala Steph.

Bryophyta-Musci

- Grimmiaceae
Grimmia trichophylla Grev.
- Dicranaceae
Campylopus bicolor (Hornsch.) Hook.f.
- Pottiaceae
Tortella calycina (Schwgr.) Dixon
- Bryaceae
Bryum argenteum Hedw.
B. billardieri Schwgr.
- Bartramiaceae
Breutelia affinis (Hook.) Mitt.
- Hedwigiaceae
Hedwigia imberbis (Sm.) Spreng.
Rhacocarpus humboldtii (Hook.) Lindb.
- Sematophyllaceae
Sematophyllum homomallum (Hpe.) Broth.

Lichenes

- Collemaaceae
Collema sp.
- Stictaceae
Sticta crocata (L.) Ach.
- Cladoniaceae
Cladonia furcata (Huds.) Schrad.
C. aggregata (Sw.) Eschw.
C. chlorophaea (Flk.) Spreng.
C. retipora (Labill.) Fries
- Parmeliaceae
Parmelia rutidota Hook.f. and Tayl.
P. imitatrix Tayl.
P. conspersa Ach.
P. perlata (L.) Ach.
- Usneaceae
Siphula caesia Muell. Arg.
- Caloplacaceae
Caloplaca aurantiaca (Lightf.) Fries

Pteridophyta

- Ophioglossaceae
Ophioglossum coriaceum A. Cunn.
- Pteridaceae
Cheilanthes tenuifolia (Burm.f.) Swartz
Anogramma leptophyllum (L.) Link
Adiantum aethiopicum L.
- Aspleniaceae
Asplenium flabellifolium Cav.
A. praemorsum Swartz

Angiospermae

- Scheuchzeriaceae
Triglochin centrocarpa Hook.
- Gramineae
Aira caryophyllea L.
Poa caespitosa Forst.
- Cyperaceae
Lepidosperma effusum Benth.
- Centrolepidaceae
Brizula muclleri Hieron.
Centrolepis glabra (F. Muell) Hieron.
- Philydraceae
Pritzelia pygmaea (R. Br.) F. Muell.
- Liliaceae
Bulbine semibarbata (R. Br.) F. Muell.
Chamaescilla corymbosa (R. Br.) F. Muell.
Stypandra grandiflora Lindl.

Amaryllidaceae
Tribonanthes variabilis Lindl.
Hypoxis glabella R. Br.
H. occidentalis Benth.

Orchidaceae
Corybas dilatatus Rupp and Nicholls
Pterostylis nana R. Br.
Cryptostylis ovata R. Br.

Aizoaceae
Carpobrotus aequilaterus (Haw) N. E. Br.

Portulacaceae
Calandrinia pygmaea F. Muell.
C. calyptrata Hook.f.

Caryophyllaceae
Spergularia rubra (L.) J. and C. Presl

Droseraceae
Drosera glanduligera Lehm.

Crassulaceae
Crassula pedicellosa (F. Muell.) Ostenf.
C. macrantha (Hook.f.) Diels and Pritzel
C. sieberiana (Schultes) Druce

Pittosporaceae
Sollya fusiformis (Labill.) Briq.

Papilionaceae
Trifolium dubium Sibth.

Geraniaceae
Geranium pilosum Forst.
Pelargonium drummondii Turcz.

Oxalidaceae
Oxalis corniculata L.

Myrtaceae
Thryptomene saxicola (A. Cunn.) Schau.
Agonis juniperina Schau.
Darwinia citriodora (Endl.) Benth.

Umbelliferae
Hydrocotyle callicarpa Bunge
H. diantha D.C.
H. blepharocarpa F. Muell.
H. hirta R. Br.
Trachymene pilosa Sm.
T. anisocarpa (Turcz.) B. L. Burt
Homalosciadium verticillatum (Turcz.) Domin

Primulaceae
Anagallis femina Mill.

Longaniaceae
Mitrasacme paradoxa R. Br.

Gentianaceae
Erythraea australis R. Br.
Villarsia calthifolia F. Muell.

Solanaceae
Solanum nigrum L.

Scrophulariaceae
Veronica calycina R. Br.
Bartsia latifolia Sibth. and Sm.

Lentibulariaceae
Polypompholyx tenella (R. Br.) Lehm.

Rubiaceae
Galium murale (L.) All.

Stylidiaceae
Levenhookia dubia Sond.
Stylidium corymbosum R. Br. var. *proliferum*
 Benth.
S. calcaratum R. Br.

Compositae
Helipterum cotula (Benth.) D.C.
Quinetia urvillei Cass.
Rutidosia multiflorus (Nees) B. L. Robinson
Angianthus tenellus (F. Muell.) Benth.
A. humifusus (Labill.) Benth.
Hypochoeris glabra L.
Cenia turbinata (L.) Pers.
Podolepis lessonii (Cass.) Benth.

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4.—The Subterranean Freshwater Fauna of Yardie Creek Station, North West Cape, Western Australia

By G. F. Mees*

Manuscript received—22nd August, 1961

The fauna of the wells of Yardie Creek Station consists of four species: a Synbranchid eel which is described and named in this paper, the Eleotrid fish *Milyeringa veritas*, and two species of Atyid shrimps. All these species show the usual characters of cave fauna: loss of eyes and of pigment. The fact that all species represent endemic genera suggests a considerable antiquity of this fauna. A discussion of the geology of the area is given, but no conclusion as regards the actual age of the fauna is reached.

Historical Review and Introduction

The occurrence of a specialised subterranean freshwater fauna at North West Cape was first made known by Whitley (1945). In October 1944, Mr. Whitley visited Yardie Creek Station, and was told by the station owner, Mr. E. Payne, of the occurrence of blind fishes in the Milyering Well, one of the wells on the station. Mr. Whitley and Mr. Payne paid a visit to the well, and Mr. Payne climbed down into it and managed to scoop up in his hat one specimen out of about a dozen present at the time. Subsequently this specimen became the type of *Milyeringa veritas* Whitley.

Whitley (1945) gave some particulars about the Milyering Well, and suggested that a subterranean river might seep through its limestone walls. In subsequent years Whitley mentioned the species *Milyeringa veritas* a few times in publications, and in recent years additional specimens were received by the Western Australian Museum. Some years ago live specimens were on show in the annual Wildlife Show in Perth, organised by the Western Australian Naturalists' Club.

Nothing essential was added to knowledge of this subterranean fauna until 1958 when Mr. Alf Snell, who had visited Yardie Creek Station as maintenance man of a shearing team, found amongst a sample of *Milyeringa*'s he had collected some shrimps. He presented these to the Australian Museum, Sydney, whence they were forwarded for identification to Dr. L. B. Holthuis of the Leiden Museum (cf. Anon. 1959). Additional specimens collected by Mr. Snell in May 1959, were donated to the Western Australian Museum, and were also sent to Dr. Holthuis.

During one of his visits to the Western Australian Museum Mr. Snell also mentioned the observation of "blind" eels in one of the wells at Yardie Creek Station, of which, notwithstanding many efforts, he had not managed to catch a specimen.

It was mainly with a view to obtaining material of this eel, but also to get larger series of the known animals and to gain a general idea about their habitat, that from the end of July 1959 onwards Mr. A. M. Douglas and I spent ten days on Yardie Creek Station. The results of this stay were satisfactory, a specimen of the eel was obtained, and series of shrimps and *Milyeringa veritas*. Besides, collections of birds, reptiles, and insects were made.

In May 1960 another short visit was made and, thanks to Mr. Douglas's nocturnal activity, a second eel was collected.

In the meantime Holthuis (1960) described the shrimps, which he found to belong to two different, but related species. Hence, the fauna of the wells, as at present known, consists of four species: two shrimps, a goby and an eel. Though one must always remain prepared for surprises, I consider it unlikely that more species occur and believe that the macrofauna of these subterranean waters is now completely known.

In this paper, besides descriptions and notes on observations, the results of investigations into the following three problems are given:—

1. How long has the habitat where this fauna is found been in existence?
2. How different, morphologically, are the cave forms from their presumed ancestors living outside the caves?
3. What are the chemical and physical properties of the habitat?

A correct answer to these questions would mean a knowledge of how long it has taken the cave fauna to develop from its presumably eyed ancestors into what it is now, in other words, of the speed of evolution, or better, morphological change, that has occurred under these very specialised conditions. It is perhaps as well to add here that I have failed because no certainty could be obtained that this fauna has evolved in the place where it is now living.

Description of Habitat

The area under discussion is the north-western part of the North West Cape Peninsula (Fig. 1). The Cape Range, which reaches up to the lighthouse at Vlaming Head, forms the backbone of the peninsula. On the outside of the range is a platform of between 1½ and 3 km wide, and along the sea coast is a narrow line of sand dunes. It is evident that on many places fresh sand has been blown quite recently over the older coastal platform.

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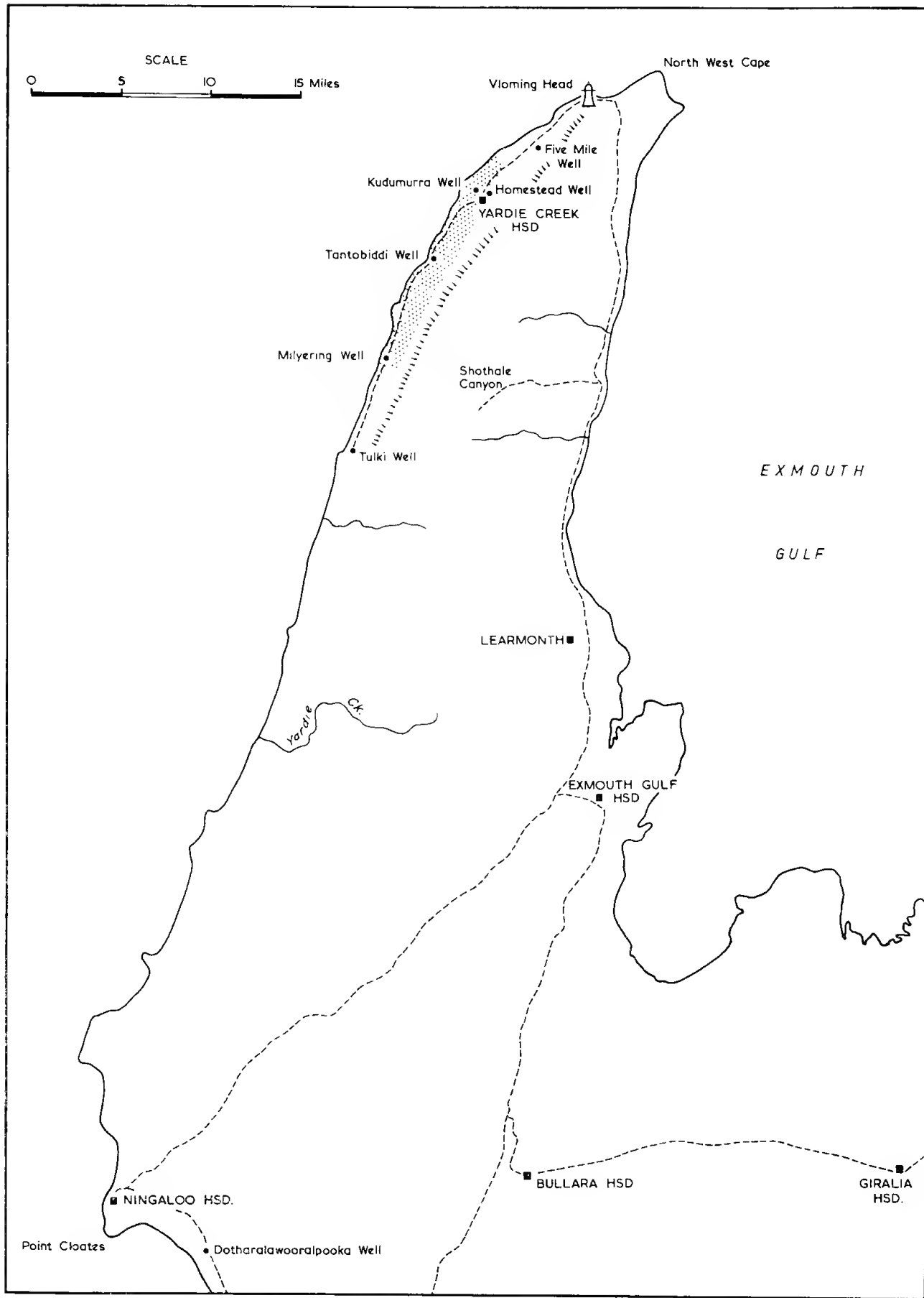


Fig. 1.—Map of the North West Cape Peninsula. The area in which the subterranean fauna is known to occur is dotted.

It is this coastal plain or platform that is of interest, because that is where the wells are sunk. The whole platform is very flat and stony, and in many places small and shallow sink holes occur which show, as do the artificial wells, that the base of this plain consists of almost pure coral rock, brownish white in colour, mixed with fossil shells, etc. The surface of the platform is about two metres above water level.

This whole layer of coral rock is apparently traversed by crevices, small holes, and connecting corridors so that an extensive subterranean network of waterways exists, which forms the habitat of the fauna under discussion. More arguments for regarding the structure as this, and not, for example, as a subterranean river (as Whitley 1945, thought), follow below.

The platform extends along the whole outside of the peninsula, but to the south I have only been as far as the Tulki Well, and I do not know if the structure farther south is identical. However, there is a length of at least fifteen miles of coral-rock platform.

In this platform, at distances of five miles apart, sheep wells have been sunk, which are, from north to south: Five Mile Well (Chugorie Well on the Admiralty Chart), Kudumurra Well and Homestead Well (these two are only a few hundred metres apart), Tantabiddi Well, Milyering Well, Tulki Well*. Holthuis's statement that the Milyering and Kudumurra Wells are 20 miles apart is a slip, for their actual distance is 10 miles.

We visited and climbed down all these wells, but only in three of them cave fauna was found, and descriptions of these three follow here.

The Milyering Well (Fig. 2) is hacked out in the coral stone; the upper rim is cemented, but lower down the coral stone was apparently considered solid enough by the builders and remains uncovered. This makes climbing down easy because everywhere there are small dents and holes in the sides which allow one to get a good grip. Normally the well is covered by a few sheets of corrugated iron. Though the cemented rim has a diameter of not over a metre, lower down the well is somewhat wider. The water surface is about two metres down, and the water in the well is not over about 50 cm deep, on a cup-shaped bottom. But in the sides of the walls, on and just below the water surface, are some crevices, water channels, the places through which visiting *Milyeringa's* enter and leave the well.

A mill is on top of the well, and pumps the water in a biggish reservoir from where two pipes lead on to two drinking troughs. The water is very tasteless, which is partly caused by the high temperature, and partly by a fairly high salinity (slightly brackish). The temperature, measured several times a day in the first week of August, 1959, and again on 16th May, 1960, was about 27° C.

*The Kudumurra Well is called Kurumuru Well on the Admiralty Chart No. 3187: Mangrove Islands to North West Cape, new ed. 1915. Kurumuru may well be the more correct spelling, but the people who gave these names have gone for ever and their meaning has been forgotten.

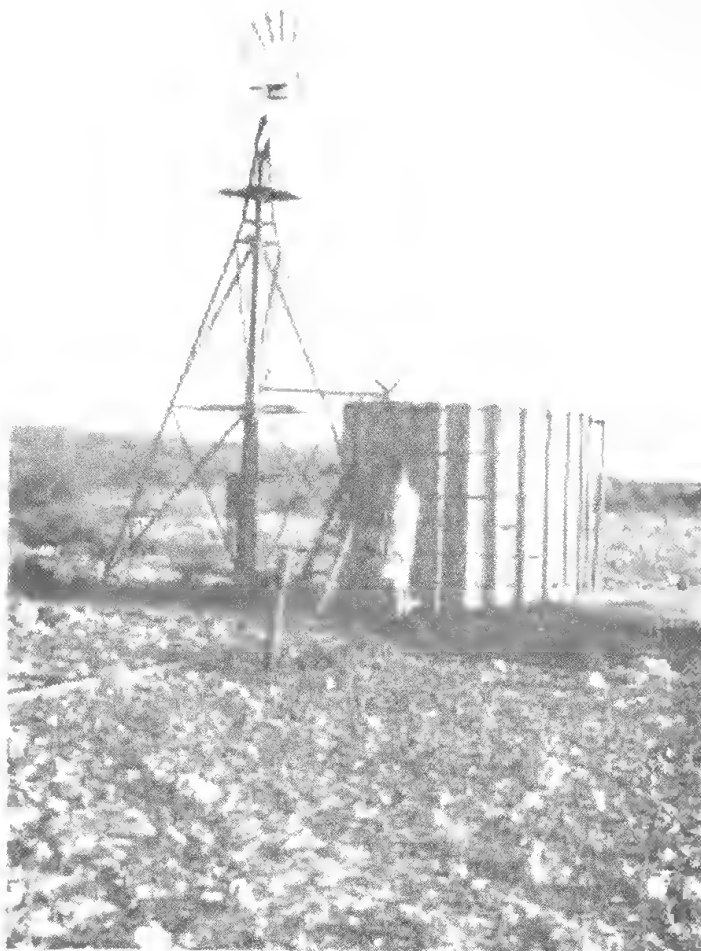


Fig. 2.—Mr. Douglas at the Milyering Well, 16.V.1960. Note the numerous blocks and pieces of coral stone that cover the platform.

A further discussion, viz. of the water movements and of the composition of the mud on the bottom follows after.

The Tantabiddi Well is a natural cavity that either was already open, or of which part of the roof has been removed. Now it is a little pool with several square metres of water surface, partly vaulted over. In two directions one sees deep tunnels or shafts, which, however, lead upwards, and therefore are dry and cannot be used by aquatic animals. The pool has a greatest depth of about half a metre and the bottom is covered with mud. There are no open connecting channels; this is important in connection with the distribution of the fauna as I shall explain later on. There is the usual Southern Cross windmill which, however, is not straight above the waterhole, but some little distance away. Probably because of its being open, the temperature of the water is slightly lower than in the other wells, about 24° C. in the first week of August, 1959. As the analysis (Table I) shows, the water is definitely less brackish than that of the Milyering Well, which is doubtless caused by the fact that rainwater has free access to this well.

The Kudumurra Well is the most prosaic looking of the three, as it is entirely cemented. The water-level is at about 1.75 m depth, and about 20 cm lower down the cemented tube

which forms the well ends, and rests on some horizontal wooden joists. The water is not over 50 cm deep and, just as in the Milyering Well, crevices and channels seem to run in various directions. The Southern Cross windmill is not above the well, but at its side, some metres away. Inscriptions on the rims of this and other wells show that they were constructed in 1913, and not in the early 1920's as Whitley (1945) would have it. The temperature of the water in this well, in August, 1959, was 29-30° C (84-86° F), on 17th May, 1960, it was 28.3° C (83° F).

TABLE I
Certificate of Analysis

Date received: 1st September, 1959.

Result of Analysis:

Marks:	Tantabiddi Well	Milyering Well
Reaction	Neutral	Neutral
pH	7.5	7.1
<i>Mineral Matter</i>		<i>Parts per million</i>
Calcium, Ca	113	126
Magnesium, Mg	141	188
Sodium, Na	999	1414
Potassium, K	36	53
Bicarbonate, HCO ₃	336	316
Carbonate, CO ₃	nil	nil
Sulphate, SO ₄	240	358
Chloride, Cl	1810	2550
Nitrate, NO ₃	3	3
Silica, SiO ₂	15	11
Iron oxide, Fe ₂ O ₃	less than 0.1	less than 0.1
Aluminium oxide, Al ₂ O ₃	5	10
Phosphate, PO ₄	0.4	0.2
	3698	5029

Assumed combination on evaporation at N.T.P.

Calcium carbonate, CaCO ₃	276	259
Magnesium carbonate, MgCO ₃	nil	nil
Sodium carbonate, Na ₂ CO ₃	nil	nil
Calcium sulphate, CaSO ₄	9	75
Magnesium sulphate, MgSO ₄	293	382
Sodium sulphate, Na ₂ SO ₄	nil	nil
Magnesium chloride, MgCl ₂	320	434
Potassium chloride, KCl	69	101
Sodium chloride, NaCl	2537	3592
Sodium nitrate, NaNO ₃	4	4

Hardness calculated as calcium carbonate.

Total hardness	862	1089
Bicarbonate (temporary) hardness	276	259
Non-carbonate (permanent) hardness	586	830
Calcium hardness	282	315
Magnesium hardness	580	774

Sgd. R. C. GORMAN,

Deputy Government Agricultural Chemist.

Water samples were taken from all three wells, but the bottle from the Kudumurra Well unfortunately lost its contents on the way down to Perth. The result of a very full analysis of the water of the other wells is given in Table I.

There is no trace of current in the water of any of the wells, which supports my opinion of the nature of the subterranean water.

It is interesting that all three wells show tidal movements; the water moves up and down about 15 cm each day. According to my geologist friends this does not necessarily mean that an open subterranean connection with the sea exists, but rather that there are permeable layers of sand, etc., which allow the tidal influences to be felt some way inland.

The mud on the bottom of all three wells is very rich in organic matter. Particularly the Milyering Well and the Kudumurra Well, both of which are normally covered with sheets of iron, act as traps for all kinds of animals that seek shelter under the covering sheets. The first time I descended the Kudumurra Well, for example, I found a small python, *Liasis childreni*, swimming in it; if I had not saved it it would doubtless have died and added to the nutritive value of the debris at the bottom. In the mud of this same well I found bones and teeth of small mammals, and in all the wells great numbers of exoskeletons of woodlice. Woodlice live in some numbers under the covers of the wells, and fall in the water regularly.

It is likely that, because of these favourable factors, the concentration of fish and shrimps in the wells is greater than it is elsewhere in their subterranean domain.

Fauna

Family SYNBRANCHIDAE

Anommatophasma genus novum*

Superficially very similar to the eel from Hoctun Cave near Chiehen Itza, Yucatan, described by Hubbs (1938) as *Pluto infernalis*, hence to the genus *Synbranchus*, but differs from that species as well as from all other members of the suborder Synbranchoidei by the position of the anus, which is in the anterior half of the body.

Type species:

Anommatophasma candidum species nova

A slender Synbranchid adapted to life in total darkness in caves. Head comparatively short, its height about half its length; upper surface of head behind snout swollen, with a shallow longitudinal groove in the middle; head deeper than any other part of the body and therefore fairly well defined; mouth comparatively large, cleft in lateral view about two-fifths of length of head; lips thick, especially anteriorly; teeth fairly strong, laterally in both jaws in a single row, anteriorly in a band of three or four rows deep; a narrow band of teeth, parallel to the jaws, on a ridge on each side of the palate; tongue well developed, anteriorly free and rounded to slightly truncate, without teeth; one pair of very small nostrils at the tip of the snout in the upper lip, a second much larger pair of nostrils on upper surface of snout just before elevation of forehead, roundish, each one covered by a dermal flap that is attached on its antero-lateral rim; eyes absent, but antero-ventrally of the second pair of nostrils is a subcutaneous concentration of what appears to be nerve tissue, and which may well represent vestiges of eyes; several pairs of mucous pores are present on the head but they are difficult to see, one fairly conspicuous pair is on the snout half way between the first and the second pair of nostrils; throat with some longitudinal dermal folds; gill opening rather wide, transverse, the covering skin lunate in shape; four pairs of gills, well developed; body long and

* From *ανομματος* = without eyes, and *φασμα* = apparition, phantom.

slender, roundish, the last few centimetres of the tail compressed; anus in anterior half of the body; lateral line distinct and continuous to near the tip of the tail, but I have been unable to find pores in it; no fins except a thin rayless fin membrane near and round the tip of the tail, in which I have been unable to detect even the vestiges of rays, but at the tip of the tail four or five hypurals are present.

Material. Two specimens.

P 4917 Tantabiddi Well, Yardie Creek Station, North West Cape, 31.VII.1959. Type.

Total length 370 mm, length of head and body (to anus) 150 mm, length of head from tip of snout to gill opening 20 mm, cleft of mouth from tip of snout to posterior border of maxilla $9\frac{1}{2}$ mm.

P 4918 Tantabiddi Well, Yardie Creek Station, North West Cape, 17.V.1960.

Total length 316 mm, length of head and body (to anus) 121 mm, length of head from tip of snout to gill opening $16\frac{1}{2}$ mm; cleft of mouth from tip of snout to posterior border of maxilla 7 mm.

Colour. The colour in life is a very striking pure white. In a captured specimen we noticed that in some parts a faint pinkish tone appeared that was not originally present; presumably this was caused by damage of small bloodvessels as a result of its capture. Microscopic examination revealed the presence of dispersed pigment in the skin which is irregularly but more or less evenly distributed over the whole body and does not show any particular pattern.

Abundance. Besides the Tantabiddi Well, where our two specimens were obtained, one example was observed in the Milyering Well. Though we have not seen specimens in the Kudumurra Well the species has been reported to occur there by one of the stationhands. The limited number of observations conclusively shows that this eel is far less plentiful than *Milyeringa* though there is no reason to regard it as particularly rare.

The explanation of the fact that in the Tantabiddi Well only eels were found, and no other cave fauna, is probably that this well, contrary to the other two wells, has no open connections with subterranean waters. Such connections as exist are filled with mud and debris, through which the eels are able to move, but not the free-swimming *Milyeringa*'s and shrimps.

Discussion. From the preceding description it will be clear that in all characters, except those which are evidently connected with life in darkness and which it shares with *S. infernalis**, this species fits very well in the genus *Synbranchus*, but for the anterior position of the anus.

The position of the anus in the Synbranchiformes has hitherto been regarded as of great systematic importance, but it seems now that the value of this character has been overesti-

* Reasons for placing "*Pluto*" *infernalis* in the genus *Synbranchus* are given in a later section of this paper.

mated. Reference to the position of the anus in the diagnosis of the suborder Synbranchoides as given by Regan (1912) and of the family Synbranchidae as given by Weber & de Beaufort (1916), to mention but a few authors, should be eliminated. It is interesting to note that Berg (1955) did not mention the position of the vent in the diagnoses of any of the subdivisions of the order.

On the other hand, it seems unlikely that the anterior position of the anus in *Anommato-phasma* would be advantageous in cave life, hence be adaptive (more about this will be said in the section on convergence and nomenclature). Perhaps, however, food conditions and the predator-free cave life may have been responsible for a shortening of the digestive tract. Anatomical work and a study of feeding habits and food may in future cast new light on this problem. Until these points have been cleared I feel perfectly justified in attaching generic importance to the character. This point of view finds mild support in the fact that both the other fish and the shrimps inhabiting this habitat have developed into indigenous genera.

As far as the relationships of *Anommato-phasma candidum* are concerned, the obvious species to consider is *Synbranchus bengalensis* (McClelland), which is the only other Synbranchid eel known to occur in Western Australia*.

The genus *Synbranchus* is in need of a revision, and the various nominal species are very similar to each other. I have compared specimens of *S. marmoratus* and *S. bengalensis* and found that *S. marmoratus* apparently differs from *S. bengalensis* by having a much narrower gill-opening which is concealed in longitudinal skin-folds, in having relatively larger eyes, and more vertebrae. One specimen, however, is very near *S. bengalensis* but differs by having a slightly larger number of vertebrae; the anus is slightly more posterior in position*. *Anommato-phasma* has a wide gill-slit, as has *S. bengalensis*, but unfortunately *S. infernalis* has, as Hubbs's figure shows, also a wide slit though it is supposed to have been derived from *S. marmoratus*.

* Whitley (1948, 1960) has resurrected the name *Synbranchus gutturalis* Richardson for specimens from Australia. As he has apparently never given reasons for this I do not follow him. I do not belong to that group of zoologists who regard the mere fact of the occurrence of an animal in Australia in itself as sufficient reason to separate it nomenclaturally.

* This specimen bears on its label the name *Synbranchus chilensis*, Chili, Frank 1849, R.M.N.H. no. 3899. *S. chilensis* is apparently a manuscript name that has never been published. The only *Synbranchus* at present known from the west coast of South America is *S. marmoratus* which, however, has not been recorded from Chili, Peru being its known southern limit. In view of the somewhat obscure origin of the specimen (localities supplied by dealers are notoriously untrustworthy; as far as Frank is concerned, see Gijzen 1938, p. 180), it seems best not to attach much importance to this. Though the specimen seems to show some slight differences from *S. marmoratus*, the fact that it has the same number of vertebrae points to its belonging to that species. The mention of the name *S. chilensis* in this discussion must not be interpreted as a validation of this name for use in zoological nomenclature (cf. Copenhagen Decisions on Zoological Nomenclature, 1953, p. 63, § 114).

The differences in position of the anus between *Synbranchus* and *A. candidum* are quite striking:

<i>S. marmoratus</i> ("chilensis").			
preanal length: postanal length	10	:	3
<i>S. marmoratus</i> .			
preanal length: postanal length	8	:	3
<i>S. bengalensis</i> .			
preanal length: postanal length	8	:	3
<i>A. candidum</i> .			
preanal length: postanal length	2	:	3

Some of the specimens were X-rayed. The number of vertebrae as counted from X-ray photographs is:

	body	tail	total
<i>S. marmoratus</i> (R.M.N.H. no. 3899)	84	+c.54	c.138
<i>S. marmoratus</i> (R.M.N.H. no. 16352)	87	+ 48 [†] (tip of tail damaged)	135 [†]
<i>S. bengalensis</i> (R.M.N.H. no. 7146)	75	+ 54	129
<i>S. bengalensis</i> (same regd. no.)	77	+c.53	c.130
<i>A. candidum</i> (W.A.M. no. P 4917)	51	+ 111	162
<i>A. candidum</i> (W.A.M. no. P 4918)	54	+ 109	163

These figures show that the number of vertebrae is a useful systematic character in the group. Because I have been unable to examine this character in all species of the genus *Synbranchus* and related genera, I have not mentioned the large number of vertebrae of *Anommatophasma* in the diagnosis of that genus though I note that according to Regan (1912) *Synbranchus* has 127-137 vertebrae. It is clear, however, that *A. candidum* differs from the species of *Synbranchus* that were examined both in having a decreased number of vertebrae in the body and an increased number in the tail.

The description of *Typhlosynbranchus boueti* Pellegrin (1922) shows that in one respect, the presence of only three pairs of gills, that genus is more different from *Synbranchus* than is *Anommatophasma*, but it has the anus in the posterior third of the body. From *Anommatophasma* it further differs by the strong pigmentation and the small gill-opening.

Comparison of *Anommatophasma* with other genera of the Synbranchidae is superfluous.

Family ELEOTRIDAE

Milyeringa veritas Whitley

Milyeringa veritas Whitley, Aust. Zool. 11, 1945, p. 36, Fig. 15—Milyering, Yardie, 20 miles south-west of Vlamingh Head, North West Cape, Western Australia.

Milyeringa; Whitley, Aust. Zool. 11, 1947 (June 20), p. 146 (Western Australia); Whitley, in: Biogeogr. Ecol. Aust., 1959, p. 142, 146 (Fig. 3 no. 34), 147 (in a well in the North West Cape area); Holthuis, Crustaceana 1, 1960, p. 48 (Kudumurra Well).

Milyeringa veritas; Whitley, W. Aust. Nat. 1, 1947 (Dec. 15), p. 53 (Greyfan Fluviatunula); Whitley, W. Aust. Fish. Dept., Fish. Bull. 2, 1948, p. 28 (Western Australia); Whitley, Aust. Mus. Mag. 10, 1951, p. 162 (Milyering); Whitley, Aust. Mus. Mag. 11, 1954, p. 151, 153, Fig. (north-western Australia); Whitley, Proc. Roy. Zool. Soc. N.S.W. 1954/55, 1956, p. 42 (Australia); Holthuis, Crustaceana 1, 1960 (Jan.), p. 47 (Milyering Well); Whitley, Nat. Freshw. Fish. Aust., 1960 (Nov.), p. 121 (North West Cape); Mees in Ann. Rep. W. Aust. Mus. 1959-60, 1961, p. 23 (North-west Cape); Ride & Serventy, in Little (editor): Off. Yearb. W. Aust. 1960, no. 2 (n.s.), 1961, p. 67 (wells and subterranean channels in the North West Cape area).

This curious goby was described and figured by Whitley, to whose notes I have little to add. Instead of D IV-9, A 9, it would be better to write D IV-8½, A 8½. The scales are reduced, and entirely absent from the head; there are about 28 rows in a longitudinal line. The variation in size in our series of about 50 specimens is from 30 mm to 42 mm in standard length.

Colour. Yellowish white in life and health. The brain is visible through the upper surface of the head as a more or less triangular dark patch. The fins are white as the rest of the body. The flesh colour of the fins recorded by Whitley (1945, 1960) must be due to the same cause referred to under *Anommatophasma candidum*. I have been unable to detect any pigment in the skin.

Abundance. At our arrival on 29th July, 1959, we found about half a dozen specimens of *Milyeringa veritas* in the Milyering Well. We caught them, and, as the well is fed by subterranean channels, the original number was gradually restored, so that during the afternoon and evening we could harvest several times. However, in my notes of 5th August, it is stated that, whereas on the first day every time about six specimens could be taken, now we did not find more than one or two during each visit. It is out of question that, by taking specimens from one single well, we would have been gradually depleting the whole population, but it does indicate that the fishes do not swim far or fast, that because of our activities they had become scarce in the near surroundings of the well, and that replenishment from more remote areas took place too slowly to counter-balance the influence of our collecting. On 16th May, 1960, the usual half-dozen was present again. Whitley (1945) stated that during his visit about a dozen specimens were present in the Milyering Well and that three times as many had been seen in the well, but we never found such large numbers.

In the Kudumurra Well the species is much scarcer, quite often no specimens at all were present, usually only one or two, and never more than three at a time. No specimens were ever observed in the Tantabiddi Well.

Discussion. When Whitley (1945) described *Milyeringa veritas*, he not only placed the species in a new genus, but also in a new family, though suggesting that it was: "perhaps evolved from some gudgeon similar to *Carassiops*, which is not known from Western Australia." Subsequently Whitley (1947) recorded *Carassiops compressus* from a well east of Carnarvon and added that: ". . . they indicate the probable line of descent of the interesting Western Australian blind gudgeon, *Milyeringa* . . ."

It should be remarked that the creation of a new family or other high systematic unit for a new species is about the cheapest way to escape from the trouble of finding its true affinities. In the present case one may wonder

why a new family had to be established when Mr. Whitley already suggested that *Milyeringa* was derived from *Carassiops*; in other words, if the new genus *Milyeringa* can be said or is believed to be close to *Carassiops* and not to other genera of the Eleotridae, *Milyeringa* and *Carassiops* are evidently closer to each other than either is to other genera of the Eleotridae, and therefore *Milyeringa* can certainly not be separated from *Carassiops* as a different family.

The genus *Carassiops* is nowadays regarded as a synonym of *Hypseleotris* (cf. Koumans 1953, p. 324). As I wanted to have an expert opinion on the affinities of *Milyeringa*, some specimens were forwarded to Dr. Boeseman who gave me (in litt., 13.1.1960) as his opinion that the species *Milyeringa* is closest to *Prionobutis microps* (M. Weber). *Prionobutis* is a genus of Eleotrid fishes that is supposed to be not distantly related to "*Carassiops*." *Prionobutis (Pogoncleotris) microps* occurs in New Guinea and in north-western Australia (Daly River) in fresh and brackish water. The similarity in many respects is striking, according to Dr. Boeseman, and includes general shape, particularly shape of the head, D 1.8 or 9, A 1.8 or 9, C. c. 14, V 1.5, se. e. 30, shape of mouth and tongue (rounded-truncate), dentition, papillae on snout, etc.

On the other hand, the differences between *Prionobutis* and *Milyeringa* are certainly large enough to keep the two genera separate. *Milyeringa* may or may not have been derived from *Prionobutis*, at present it is morphologically sufficiently different to be regarded as a fairly well-marked separate genus.

Family ATYIDAE

Stygiocaris lancifera Holthuis

Stygiocaris lancifera Holthuis, Crustaceana 1, 1960, p. 48—Kudumurra Well, Yardie Creek Station, North West Cape Peninsula, W. Australia.

Stygiocaris lancifera; Mees in Ann. Rep. W. Aust. Mus. 1959-60, 1961, p. 23 (North-west Cape).

This species seems to be very much the commoner of the two, for the material sent to Dr. Holthuis consisted of 147 specimens of this species as against 15 of *S. styliifera*.

As the two species were not distinguished by me the following notes may apply to either of them, but doubtless mainly to *S. lancifera*. Shrimps were common in the Kudumurra Well, but scarce in the Milyering Well and not found in the Tantabiddi Well.

They are entirely colourless transparent, with the exception of the internal organs of the thorax, which show as a yellowish mass. The contents of the intestine is visible as a straight black stripe, but many specimens have the intestine empty.

In the Kudumurra Well I often observed shrimps. In daytime it was very difficult to see them, but at night in torchlight they were more visible. They appeared to be resting, probably also feeding, on the upper surface of the wooden joists, on the walls of the well, and also on the mud of the bottom. An occasional individual would swim round freely just under the water

surface, possibly obtaining food from the surface film. There is no evidence that digging or roeting in mud takes place to any extent.

Stygiocaris styliifera Holthuis

Stygiocaris styliifera Holthuis, Crustaceana 1, 1960, p. 54—Kudumurra Well, Yardie Creek Station, North West Cape Peninsula.

Stygiocaris styliifera; Mees in Ann. Rep. W. Aust. Mus. 1959-60, 1961, p. 23 (North-west Cape).

As noted under the preceding species, the relative abundance of *S. styliifera* as opposed to *S. lancifera* is about 1:10 in the material collected. This slightly larger species seems therefore to be much less plentiful.

Geological Evidence

Largely as a preliminary to and a result of the recent intensive oil exploration in the region, the geological structure of the North West Cape Peninsula is well known (Condon, Johnstone & Perry 1953). The spine of the peninsula is formed by the Cape Range, the exposed parts of which are mainly of Tertiary age: these same authors state that the coastal platform is Recent, but they do not devote any particular attention to it.

To Dr. Logan (in litt., 16.IX.1959) I am greatly indebted for much additional information, most of which I quote verbatim:

"I examined the plain along the western piedmont of the Cape Range some years ago, and I believe that it is a wave cut platform related to a former sea level of five to six feet above present mean sea level. In a few places in the area one can observe undercut pedestals or stacks of limestone standing above the level of the platform which exhibits most of the characteristics of the undercut on the shoreward periphery of the contemporary 'reef' flat which Fairbridge and others have described at Rottnest, Point Peron and elsewhere on the Western Australian coastline. The higher sea level stand at about two metres can be substantiated by emerged shell beds, coral reefs and wave cut platforms which occur at about two metres above present sea level in the Shark Bay area. Allowing for somewhat more tidal amplitude in the vicinity of N.W. Cape the Yardie platform can be well correlated with this level; meaning that the area along the foot of the Cape Range was inundated by the sea in sub-Recent times.

Evidence all along the W.A. coastline and elsewhere in the world suggests a higher stand of sea level at about two metres above present due to eustatic causes (advance and retreat of the polar ice caps). The evidence for this eustatic sea level high is imposing and the constancy of the terrace level over wide stretches of coastline must tend to rule out local uplift as a genetic cause of this feature. One may expect slight variations in height due to local energy factors in the marine erosion of the coastline as differences in exposure to waves and tidal amplitude must inevitably cause slight variations in height of the platforms. I be-

lieve that the above explanation of the platform along the edge of the Cape Range is reasonable although one must be cautious for the Cape Range is a fold mountain which shows evidence for upwarping in the Pliocene, Pleistocene and possibly the Recent.

The two metre plus sea level stand of sub-Recent times has been dated in various parts of the globe by C14 dating techniques which gives ages of about 5,000 B.P.

The actual limestone outcrop along the foot of the Cape Range is similar lithologically to the Coastal Limestone along the western coast of W.A. between Geraldton and Dirk Hartogs Island; this is mainly an aeolian limestone formed by terrestrial agencies, and it dates from Pleistocene to Recent in geological age. Some of the platform may also be cut in Pliocene or Miocene limestones which occur on the flanks of the Cape Range"

The evidence that the coastal platform is not more than about 5,000 years old is quite conclusive and can be accepted without reservation. On the other hand, everything known about the speed of evolution or morphological change of animals points to its being a very slow process. Even under the extreme conditions under which the fauna under discussion lives, it is very hard to believe that morphological changes of a magnitude that demands generic separation from their presumed ancestors would have taken place in only 5,000 years. However, I quote a further paragraph from Dr. Logan's letter:

"As was found in the petroleum exploration of the Rough Range, the limestones in the N.W. Cape region are very cavernous down to about sea level, and it is not outside the bounds of possibility that the fauna developed and is living in these subterranean caverns which may have been connected to the sea at one time (for that matter they may still be in some connection) and the wells are now tapping water from these caves."

Therefore I regard it as likely that the subterranean fauna has developed in late Tertiary or in Pleistocene times, in what are now the hills, and that with the retreat of the sea during the last 5,000 years, and the subsequent emergence of the coastal platform and the decrease in salinity of the water, this fauna has been able to colonise the platform from the cavern systems in the hills.

Problems of Convergence and Nomenclature

Attention has already been drawn to the extraordinary similarity in general appearance between *Anommatophasma candidum* and *Synbranchus infernalis*.

However, whatever the true relationships between the two species may be—and the aberrant position of the anus in *Anommatophasma* suggests that they are only distantly related—it is likely that each of them has been derived from a different species of Synbranchid. Nevertheless, if morphological evidence only was considered,

the two species would probably be regarded as very closely related. Yet, what we really have is convergence because it is fairly clear that *S. infernalis* has been derived from *S. marmoratus*, whereas the possible ancestor of *Anommatophasma* was *S. bengalensis*. When applying morphological criteria without historical considerations, "*Pluto*" *infernalis* and *Anommatophasma candidum* might well be united in one genus, and their respective ancestors in a different one. Hubbs was aware of the fact that his "*Pluto*" *infernalis* has been derived from *S. marmoratus*, and therefore is historically closer related to *S. marmoratus* than that species is to the other species of *Synbranchus*, but notwithstanding that, he allowed morphological facts to prevail when he created for his blind eel a new genus.

Of the conflict between historical relationship and morphological similarity in what we please to call the "natural system," most systematists are doubtless aware, and I do not see how it can ever be solved*. It seems appropriate, however, to draw attention to the fact that in our whole system authors use nearly always words like "affinity" and "relationship," for what is actually morphological similarity. Though the jargon has changed with the times, the method is still essentially the same as that used by Linnaeus and his contemporaries, two centuries ago.

Personally I believe that ideally in a natural system actual relationship should be expressed rather than morphological similarity, but I am well aware that only in a very few cases, as that of "*Pluto*," it is possible to distinguish between the two, and even when the distinction is clear, group names (families, genera, etc.) are applied in an arbitrary manner. For example, birds and mammals are probably closer related to certain orders of reptiles than the latter are to other orders of reptiles, yet we retain the classes Aves, Mammalia and Reptilia—to do other than adopt this arbitrary (but phylogenetically incorrect) procedure would lead to nomenclatural chaos. Therefore, subjective judgment in which historical knowledge (including the fossil record if available) is weighed against morphological criteria, will continue to be the basis of our system of classification.

It seems to me that Holthuis (1960) has not found a solution of the problem. In his diagnosis of the genus *Stygiocaris* he wrote:

"The genus is closely related to *Typhlopatsa* Holthuis from Madagascar perhaps *Stygiocaris* should only be considered a subgenus of *Typhlopatsa*." I do not claim to have even the slightest knowledge of shrimps, and therefore am unable to evaluate their morphological characters. But I regard it as unlikely that blind shrimps from fresh water in Madagascar and blind shrimps from fresh water in Western Australia, separated by many hundreds of miles of ocean, would be nearer related to each other than either of them would be to some eyed species living along the coasts of Madagascar and Western Australia respectively. Instead of the words "closely related" Holthuis should have

* Of course I am aware of the existence of a large philosophical literature on the subject.

written "morphologically closest." for this morphological similarity may well be due to convergence.

Several times I have mentioned the fact that I regard certain characters as not of generic value because they are connected with life in darkness. This point of view is likely to meet with criticism because it may well be argued that any character is adaptive. However, most zoologists nowadays do not attach too much systematic significance to characters that are evidently connected with some particular way of life in animals that otherwise are morphologically close to other species. This would apply even more where a loss of characters is involved as a consequence of the absence of selective pressure for their retention.

It is on the basis of the preceding arguments that I prefer to place "*Pluto infernalis*" in the genus *Synbranchus*, so that the species should now be known as *Synbranchus infernalis* (Hubbs). The genera *Pluto* Hubbs and *Furmastix* Whitley 1951 (nomen novum for *Pluto* Hubbs, preoccupied), consequently enter into the synonymy of *Synbranchus*. It will be noted that I have based a separate genus for the Australian blind eel not on characters common to all cave fishes, but on the anterior position of the anus, a character that is unlikely to be directly connected with life in total darkness (as it is not found in *S. infernalis*, which lives under similar conditions).

Orientation

Very little can be said by me about the subject. All the "blind" species have probably lost their eyesight completely, which seems evident from the complete absence of pigmentation in the ocular region.

Nevertheless, some orientation must occur; particularly *Anommatophasma* has a habit of making straight for dark crevices when being disturbed out in the open of a well, and it seems likely that some kind of light perception exists. Tactile factors could hardly be involved in this kind of orientation. On the other hand it is well known that some other senses, like smell, are extremely highly developed in some fishes. Without experiments and anatomical investigations it will be difficult to decide if any perception of light still occurs in the species; light sensitivity (which is not sight) may well exist, it may be located in the pineal organ as is the case in other eyeless fishes, or in the rudiments.

Acknowledgments

From the section on the geology of the coastal platform of Yardie Creek Station, it will be evident how much I owe to Dr. B. W. Logan (Agricultural and Mechanical College of Texas, College Station, Texas). Discussions with Dr. J. E. Glover and with Messrs. C. W. Hassell and E. W. S. Kneebone (all of the Geology Department, University of Western Australia, Netherlands), further assisted in giving me a clear idea of the geology of the region.

The X-ray photographs were taken by courtesy of Mr. R. W. Stanford, Department of Medical Physics, Royal Perth Hospital.

To the authorities of the Government Chemical Laboratories, Perth, I am indebted for the very complete chemical analysis of the collected water samples which is reproduced in Table I.

Dr. M. Beeseman (Rijksmuseum van Natuurlijke Historie, Leiden), examined specimens of *Milyeringa*, and gave me his valuable opinion on their affinities; he also sent me on loan specimens of various species of Synbranchid eels. The manuscript was read by Drs. M. Boeseman, L. B. Holthuis and W. D. L. Ride, to all of whom I am indebted for useful suggestions.

To the keen interest of Mr. A. Snell we owe the information that with the discovery of *Milyeringa veritas* the subterranean fauna of Yardie Creek was not yet fully known. This not only led to the discovery by himself of the two species of shrimps, but ultimately also to our trip to the region and the capture of specimens of the remarkable *Anommatophasma candidum*.

Finally, both Mr. Douglas and I want to express our sincere gratitude to Mr. and Mrs. W. D'Arcy of Yardie Creek Station, who not only allowed us to come and stay with them and collect on the station but who also assisted in every possible way to make our trip the complete success it became. The same thanks have to be extended to Mr. E. Payne, owner of the station, who, unfortunately, we did not have the pleasure of meeting.

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