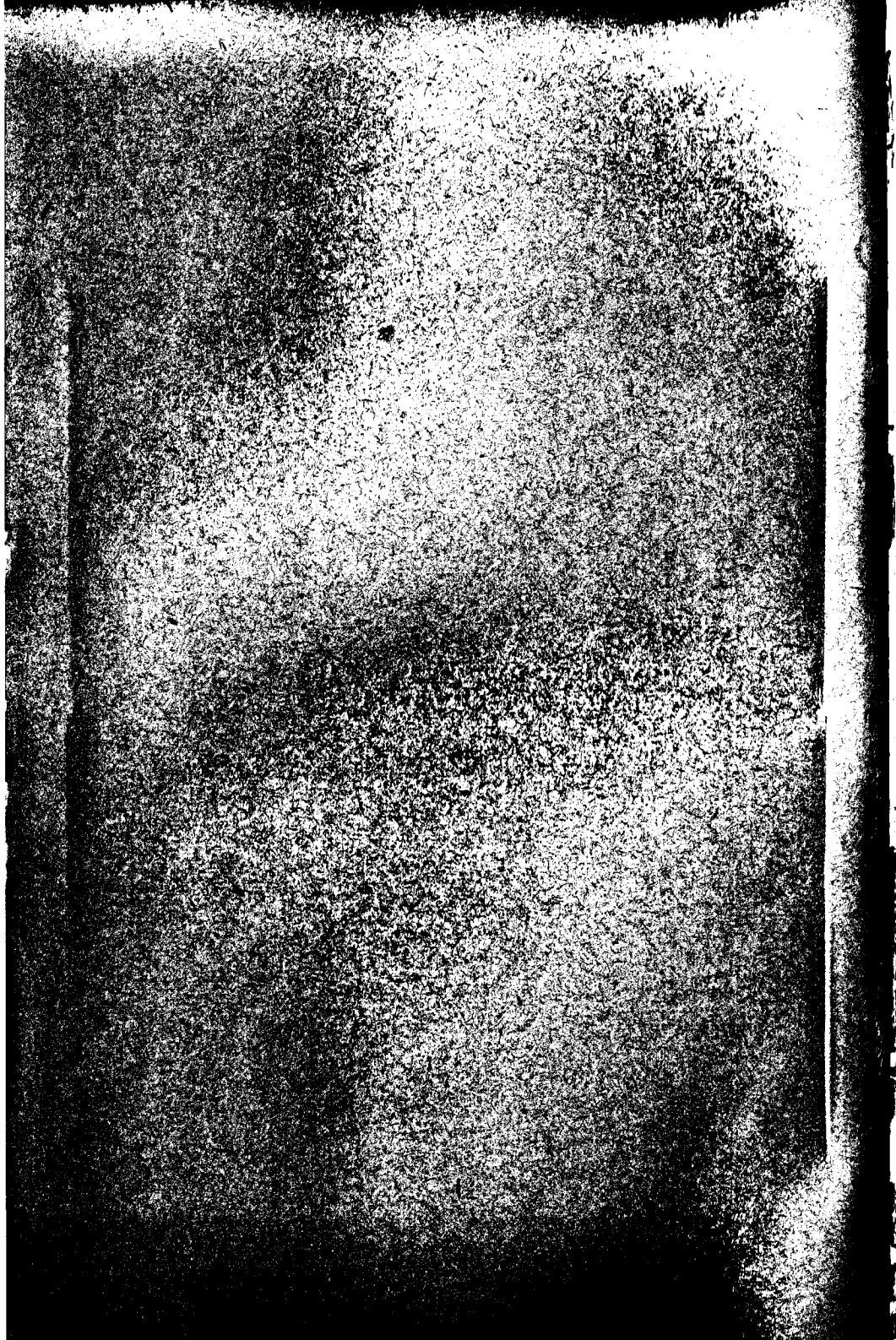

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STUDY OF THE *ODONATA* OF TASMANIA IN RELATION TO THE BASSIAN ISTHMUS.

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Introduction.

The Bassian Isthmus is the name given to that portion of land, now sunk beneath the sea, which once connected Tasmania with the mainland of Australia. Although all scientists are agreed on the previous existence of such a connection, yet there is not, so far, sufficient evidence to enable us to say, definitely and precisely, when, where and how long it existed, and at what period of past time it broke down.

A short summary of the opinions expressed on the point will perhaps make the position clear.

Professor Baldwin Spencer*(1892), on the evidence afforded by the Mammalia, concluded that "at some period during Tertiary times, ... and comparatively early in the period, Tasmania began to be gradually separated off from the mainland. . . . When Tasmania became separated off, it contained a series of forms identical, so far as *genera* are concerned, with those of what is now Victoria, and in *species* almost identical with those of Southern Victoria." And again: "We must conclude from the mammalian fauna that there has been no absolute land-connection between South-East Australia and Tasmania since practically the end of the Tertiary Period or early in Pleistocene times, as otherwise it would be impossible to account for the absence, not only of the dingo, but also of the large and specialised Diprotodont fauna, of

* Report Aust. Assoc. Adv. Sc., Hobart, 1892, pp. 117, 118.

which the Pleistocene Period saw the rise and fall upon the mainland."

The late Mr. A. W. Howitt*, in an able discussion on the Tasmanian aborigines, states: "In early Tertiary, or even late pre-Tertiary times . . . the northern part of Tasmania was relatively higher above sea-level by at least 270 feet than it is now." Later, "a period of great basaltic extrusion covered and protected many of the Older Tertiary Sediments, and culminated in a widespread subsidence to some 1,000 feet on the west coast and 700 feet on the north coast of Tasmania. . . . Subsequently there was a re-elevation of the land during Pleiocene and more recent times. . . . The commencement of this later connection of Tasmania and Victoria may be provisionally placed in the Pleiocene epoch." He also gives a map showing the 50 and 100 fathom lines for the depth of the sea over the area in question, from which it can be seen that the elevation of 270 feet mentioned, would be quite sufficient to lay bare nearly all that portion now known as Bass Straits.

Mr. C. Hedley†(1903), in a very interesting paper, shows that the marine Molluscan fauna of the southern coast-line of Australia is not continuous from east to west, but can be subdivided into two very distinct faunas, the "Adelaidean" westwards and the "Peronian" eastwards, each distinguished by the possession of many special forms. Further, though the fauna of the east coast to Cape Howe is Peronian, the fauna of Hobson's Bay and Westernport is shown to be Adelaidean. The striking conclusion is drawn, that the Bassian Isthmus must, therefore, have lasted much later, as a narrow connection between Wilson's Promontory and the North-East of Tasmania, than it did as a connection with the north-west of the island. Mr. Hedley wisely does not attempt to fix dates, but points out that the fact of these two marine faunas not yet having had time to intermingle, places the submergence of the Isthmus necessarily at a very late and, probably, post-Tertiary period.

* Report Aust. Assoc. Adv. Sc., Sydney, 1898, p.740.
† These Proceedings, 1903, p.876.

Dr. Fritz Noetling*(1910)argues ably, from his knowledge of the very low state of civilisation of the Tasmanian aboriginals, that they could not possibly have reached the island in canoes, but must have crossed over on dry land. The date of submergence of the Isthmus must, therefore, have been recent enough to allow of the passage of man across it beforehand, though the crossing of later arrivals (the Australian aboriginals and the dingo) was prevented. He gives the following approximate dates, which can be only regarded as purely hypothetical:—

Last Glacial Epoch.—60,000 years ago.

Post-Glacial Epoch.—Existence of a broad Isthmus 50,000 years ago. Submergence began 10,000 years ago, about the time that the gigantic Marsupials disappeared.

Prehistoric Epoch.—Submergence still going on, 7,000 years ago; Tasmanian aborigines arrived. Formation of Bass Straits completed about 5,000 years ago; the dingo reached Australia.

The discovery of the remains of the giant Diprotodon in Tasmania, and the strong evidence in favour of the dingo having been brought to Australia in a semidomestic condition by the Australian aborigines, make it evident that Professor Baldwin Spencer was placing the limit too far back, when he argued for the complete isolation of Tasmania since the close of the Tertiary period. On the other hand, recent discoveries of prehistoric man in Europe make it appear extremely probable that the time of man's past existence on the earth can be considerably lengthened. And since the Tasmanian aborigines are recognised as having been as low in the scale of civilisation, as any of the recently discovered prehistoric men in Europe, there is no need to accept such exceedingly close limits as Dr. Noetling would place on the time of final submergence of the Isthmus. The Diprotodon, too, was almost certainly pre-Glacial, and its existence in Tasmania does not, therefore, offer any evidence in support of Dr. Noetling's dates.

For the purposes of this paper, it will not be necessary to fix the geologic time at which the change took place. I propose simply

* Papers and Proc. Roy. Soc. Tasmania, 1910, p.261.

to divide the era under discussion into three parts, which I shall name and define as follows:—

A. PRE-ISTHMIAN.—All that period of time, including the early Tertiary period of elevation (Howitt), the period of submergence, and the final re-elevation, up to the formation of a broad land-connection, with running rivers, between Tasmania and the mainland.

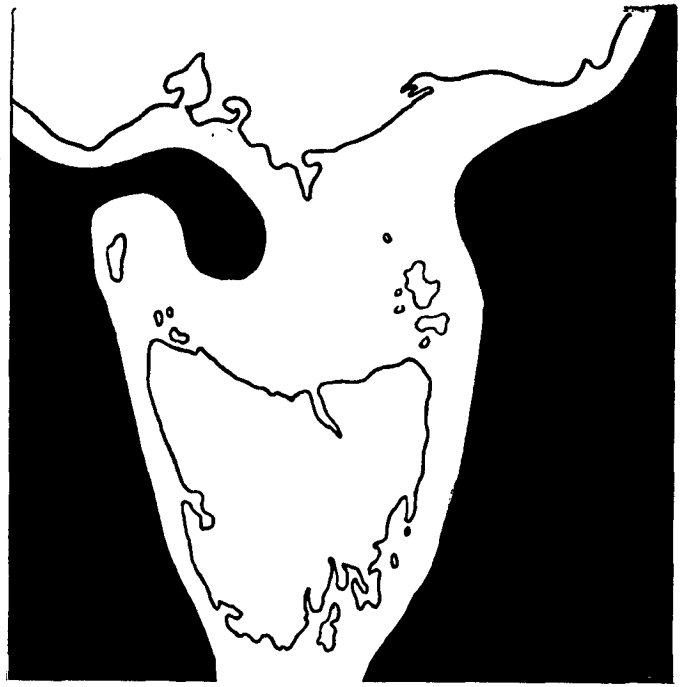

Fig. 1.—PRE-ISTHMIAN.

Fig. 1 gives a hypothetical sketch of the coast-line towards the close of this period.

B. ISTHMIAN.—The period during which a gradual narrowing of the connection took place, resulting in the formation of the narrow Isthmus on the east side, as suggested by Hedley (Fig. 2), and up to its final submergence.

C. POST-ISTHMIAN.—The period from the final submergence of the Isthmus to the present day (Fig. 3).

In the summer of 1908-9, I spent a month collecting Odonata in Tasmania, and obtained fairly comprehensive collections from many localities in the north, north-east, centre and south of the

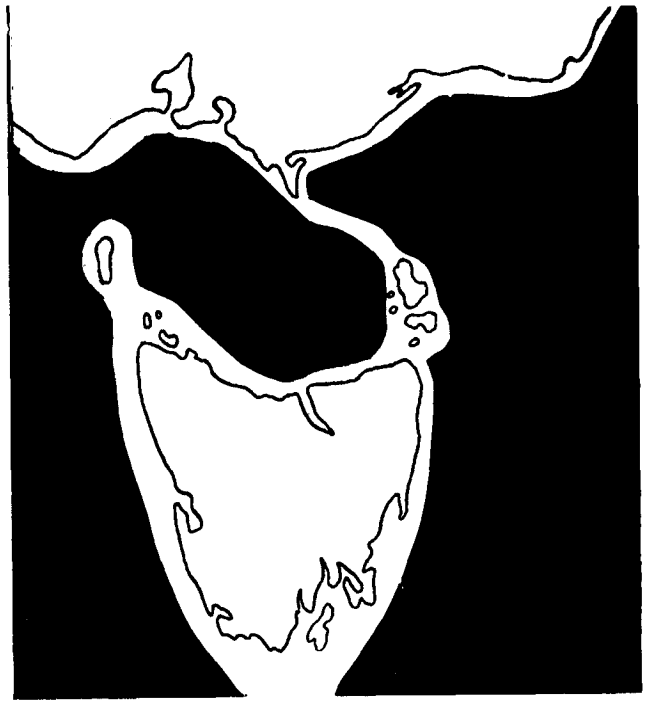

Fig. 2.—ISTHMIAN.

island. Though dragonflies were fairly numerous, the number of species obtained (nineteen) was surprisingly small.

Since then, I have received small collections from the west coast and from Ben Lomond, also a very complete collection from Mr. F. M. Littler, taken in various localities around Launceston and

along the north-western line. These have not added any new species to the list.

An examination of the material in the Hobart Museum enabled me to add further localities to my list, and also to note the occurrence of a new species in the Hobart district. The total number of species, therefore, now stands at twenty.

Though it is probable that further careful collecting may result in the addition of a few more species, yet the list, as it stands, must be by now fairly complete. As it presents some very extraordinary features which seem to me to offer very decisive evidence concerning the nature and extent of the land-connection (Bassian Isthmus), known to have existed formerly between Tasmania and the mainland, I have thought it advisable to put the facts on record.

Two facts strike one, at once, as being very remarkable in the case of the Tasmanian Odonata:—

(1) Although the island is richly watered almost everywhere by permanently running rivers, very few *Odonata* occur on them; whereas the *Odonate* fauna of the lagoons and lakes is astonishingly abundant.

(2) Many of the very commonest species, to be found all over Southern Victoria, are completely absent from Tasmania.

It occurred to me that the nature and extent of the Bassian Isthmus must have played a very considerable part in this distribution. If the Isthmus was, for a very long time, too broken or narrow to possess any permanent running water, it would follow that only those *Odonata* that were capable of breeding in stagnant water (small lagoons, pools or waterholes), would be able to cross into Tasmania, while all those species, whose larvæ require running water, would be shut out. I, therefore, made a list of the dragonflies of Southern Victoria (for which the records are very complete) and divided them into two portions.

A.—Those that have never been known to breed in still water.

B.—Those that habitually breed in still water.

This list comprises forty-two species, including all the known Victorian *Odonata* except a few exceedingly rare species only recorded from North Gippsland (Alexandra), which do not approach close enough, in their distribution, to the southern coast of that State to be taken into consideration.

Fig.3.—Post Isthmian (present day).

To these, I have added the, as yet, undescribed species from Hobart (*Austrocœschna* sp.), making a total of forty-three. Dividing these into lists A and B, and including in both A and B the species *Austrogomphus guérini*, which, although habitually breeding in slowly running water, has occasionally been observed to breed in still water, we find that list A contains twenty-four species, and list B twenty. In list B, however, we have the two geminate species, or rather subspecies, *Synthemis eustalacta* Burm., (occurring only on the mainland) and *S. tasmanica* Tillyard (occurring

only in Tasmania). From the point of view of this paper, *S. tasmanica* must clearly be reckoned as the Tasmanian portion of *S. eustalacta*. Counting, therefore, these two forms as two races of one species, list B will contain nineteen species.

I propose to give these two lists in full, and then to draw what appear to be very obvious conclusions from them:—

List A.—Species which have never been known to breed in still water (except *Austrogomphus guérini* occasionally). * present, – absent.

Name.	Victoria.	Tasmania.
Diphlebia lestoïdes Selys	*	–
Argiolestes icteromelas Selys	*	–
Argiolestes griseus Selys	*	–
Synlestes weyersi Selys	*	–
Austrolestes cingulatus Burm.	*	–
Nosoticta solida Selys	*	–
Isosticta simplex Martin	*	–
Austrogomphus guérini Ramb.... ...	*	*
Austrogomphus ochraceus Selys ...	*	–
Austrogomphus heteroclitus Selys ...	*	–
Austrocæschna, n.sp.	–	*
Austrocæschna longissima Martin ...	*	*
Austrocæschna unicornis Martin ...	*	–
Austrocæschna tripunctata Martin ...	*	–
Austrocæschna sagittata Martin... ...	*	–
Austrocæschna parvistigma Selys . .	–	*
Austrocæschna multipunctata Martin ...	*	–
Austrocæschna atrata Martin	*	–
Æschna brevistyla Ramb.	*	*
Metathemis guttata Selys	*	–
Metathemis brevistyla Selys	*	–
Metathemis virgula Selys	*	–
Hemicordulia australiæ Ramb. ..	*	–
Diplacodes hæmatodes Burm.	*	–

Total present in Southern Victoria 22
Total present in Tasmania 5
Total common to both 3
Percentage of Tasmanian to S. Victorian forms, 22·7%.

List B.— Species which habitually breed in still water (except *Austrogomphus guérini*, which does so *occasionally*).

Name.	Victoria.	Tasmania.
Austrolestes leda Selys	*	*
Austrolestes psyche Selys	*	*
Austrolestes annulosus Selys	*	*
Austrolestes analis Ramb.	*	*
Agrion lyelli Tillyard	*	*
Ischnura heterosticta Burm.	*	*
Ischnura aurora Br.	*	*
Austroagrion cyane	*	*
Austrogomphus guérini Ramb.... ...	*	*
Anax papuensis Burm.	*	
Synthemis eustalacta eustalacta Burm.	*	
S. eustalacta tasmanica Tillyard ...		*
S. macrostigma orientalis Tillyard ...	*	*
Procordulia jacksoniensis Selys ...	*	*
Hemicordulia tau Selys...	*	*
Nannophya dalei Tillyard	*	*
Austrothemis nigrescens Martin ...	*	*
Diplacodes bipunctata Br.	*	–
Diplacodes melanopsis Martin	*	
Orthetrum caledonicum Br.	*	

Total present in Southern Victoria 19
Total present in Tasmania 15
Total common to both 14
Percentage of Tasmanian to S. Victorian forms, 78·9%.

The contrast between the results given in these two lists is most striking and calls for some definite explanation. How is it that so few running-water forms, of the many found in Southern Victoria, also occur in Tasmania? How is it, on the other hand, that the great majority of those still-water forms found in Southern Victoria, also occur in Tasmania? How is it, in particular, that *of species in the same genus*, equally common and widespread in Southern Victoria, only the still-water species occur in Tasmania, while the running-water species do not? For instance out of five species of *Austrolestes*, only one, *A. cingulatus*, and that the most abundant of all in Southern Victoria, does not occur in Tasmania;

exactly that one species, be it noted, that is unable to breed in still water. Again, out of three species of *Austrogomphus*, only *A. guérini*, which habitually prefers slowly running water, and occasionally breeds in still water, occurs in Tasmania. And again, out of two species of *Hemicordulia*, that one (*H. tau*), which breeds in still water is present in Tasmania, while the equally common *H. australiæ*, which breeds only in running water, is absent.

The evidence, afforded by the above facts, seems to me to point conclusively to *the existence, for a very considerable period, of a Bassian Isthmus so narrow or incomplete, that only still-water species were able to pass across it into Tasmania.* No permanent, running streams could have been present during the time that these migrations were in progress, or, at the best, they must have been very few and far apart.

Next let us examine the exceptions to the general rule as presented above.

Firstly, the species of the genus *Austroæschna* are all running, water forms, yet three occur in Tasmania, and one of these is peculiar to the island. Coupled with this, is the fact that the running-water species, *Æschna brevistyla*, is also abundant there.

The answer to this anomaly, lies in the admittedly great antiquity of the *Æschninæ*. As these genera occur on both sides of the present barrier quite abundantly, and their larvæ cannot breed in still water (that of *Æschna brevistyla* prefers *slowly* running water, but all the species of *Austroæschna* require fairly fast, running water), it seems fair to argue, that their appearance on the scene took place at an earlier period than that of the other groups in question, at a time when the Bassian Isthmus was large and well-supplied with running streams. The fact that Tasmania also possesses, in the undescribed species of *Austroæschna*,* its only truly autochthonous species, points to the greater antiquity of this genus, compared with those whose species have remained undifferentiated.

I am of opinion that both *Austroæschna* and *Æschna* arose from a common Mesozoic ancestor, which, first of all, differentiated into

* The description of this species will shortly be published.

two main types, represented at the present day by the two main divisions of the *Æschnine* stem, viz., the *Brachytronini* (to which *Austroæschna* belongs) and the *Æschnini*. Of these, the *Æschnini* soon became dominant in all the regions of the earth except the *Australian*, while the *Brachytronini* decreased rapidly everywhere except in Australia, where (like the Marsupials) they enjoyed an uninterrupted development, and increased to form the large genus *Austroæschna* and its allies. Somewhat later, the *Æschninæ*, spreading rapidly through the Neotropic Region, sent out a few vigorous species down into Archiplata, and reached across into a temperate Antarctica. Finally, a single species, *Æschna brevistyla*, found its way into New Zealand, and also into Tasmania, and crossed the Bassian Isthmus, while it was still large and supplied with running streams. The fact that *Æschna brevistyla* is so abundant in Tasmania, and becomes rapidly rarer as we go northwards, finally failing to reach the extreme north of the continent, is a strong argument in favour of this supposition, and against the theory, held by Dr. Ris, of the origin of *Æschna brevistyla* from a common parent with the tropical *Anaciæschna jaspidea*.

Next, let us turn to the very extraordinary distribution of the *Libellulinæ* of the region under survey. In Southern Victoria, the only really common species are the three species of *Diplacodes*, which are abundant everywhere along the coast and inland also. *Orthetrum caledonicum* is abundant in the warmer parts, but gets rare along the colder southern coast. *Nannophya dalei* and *Austrothemis nigrescens* are distinctly *rare*. Yet, of all these species, which breed equally freely in still water, only the two rarest occur in Tasmania. We can only conclude that the commoner *Diplacodes* and *Orthetrum*, both known to be offshoots from tropical genera, *did not reach their present southern limit until after the disappearance of the Bassian Isthmus*. It would follow, that *Nannophya* and *Austrothemis* are much older genera, which were present in Tasmania before the Isthmus disappeared. *Nannophya* is known to be an archaic genus, with a somewhat discontinuous distribution. *Austrothemis* is a puzzle, having no very close allies, and only one

species, confined to the southern parts of Australia. There seems very little doubt that it, too, must be a remnant of some ancient Libelluline group now almost extinct.

Not less extraordinary than the case of *Diplacodes*, is the failure of the strong-flying and very abundant still-water species, *Anax papuensis*, to appear in Tasmania. This species may often be seen flying in the streets of the city of Melbourne, and it seems that it can only be a matter of time before it must establish itself in Launceston, considering the frequent communication between the two ports. The fact that it has failed, so far, to negotiate 200 miles of sea, with islands *en route*, shows how very seldom *Odonata* are dispersed across even narrow straits. Apart from a strong tendency to migrate, exhibited by a few *Libellulid* genera, there seems no reason to suppose that dragonflies are ever carried far from their breeding grounds. When storm or wind arises, they immediately seek shelter; indeed, they do so usually some time before the disturbance breaks upon them.

Argiolestes icteromelas and *Hemicordulia australiæ* are both very abundant in Southern Victoria; but, as they breed in running water, their inability to cross over is explainable on the hypothesis already offered.

The case of *Hemicordulia tau* has some special features. This species is exceedingly abundant in Victoria, but quite rare in Tasmania. It is only in occupation of occasional pools and waterholes, and, in particular, of artificially constructed dams. It is the only southern Australian species which has developed a migratory tendency. Particularly in the autumn, when a second brood appears, it is recorded at intervals of a few years apart, as appearing in thousands over large areas, and travelling for many miles. I am strongly of opinion that *Hemicordulia tau* is the most recent addition to the *Odonate* fauna of Tasmania, and that the scanty colonisation of the island, by this species, has been brought about by the successful passage of Bass Straits by portion of one of these migratory swarms, probably within the last few years. The fact that it has not yet colonised the large swamps and lagoons, is a strong argument for this view.

Let us next consider the case of the *Synthemina*, of which the two still-water species, *S. eustalacta* and *S. macrostigma*, are represented in Tasmania, while the running-water species of the genus *Metathemis* do not occur there. The typical form of *S. tasmanica* discovered by me at St. Patrick's River, differs very considerably, both in size and colouration, from *S. eustalacta*. But I also found, at Launceston, breeding in still-water, a form whose colouration was almost exactly that of *S. eustalacta*, and whose size was intermediate between the latter and typical *S. tasmanica*. We see, therefore, that *S. eustalacta* crossed over as a still-water form, but that it is now developing into a running-water species on the island, and is assuming, with the change of habit, the darker and duller colouration already attained by *Metathemis* on the mainland. *S. macrostigma*, on the other hand, still keeps to the swamps, and shows no variation from the mainland form.

The *Synthemina* are admittedly the most archaic of the *Corduliinæ*. There can be little doubt that they attained their present group-characters at least as early as the beginning of the Tertiary period. It seems probable, therefore, that they may have crossed to Tasmania during the very earliest part of the Pre-Isthmian period (the period of Howitt's "first elevation"). Such a supposition is in keeping with their comparative rarity on the island, if we see in all the other still-water *Libellulidae* a more recently arrived band of competitors.

Metathemis is a specialised offshoot of *Synthemis*, and only breeds in running water. The fact that this genus keeps to the high lands, and only approaches the coast where it is very hilly, prevents us from using it as an argument for the absence of running water on the land-connection during Howitt's "first elevation" period.

Summing up, we now have the following facts:—

(1) Of the running-water forms, only 22% have succeeded in passing from Victoria to Tasmania. These consist of the most archaic forms found in the island (*Austroæschna*, *Æschna*). Hence only during the earliest period of the land-connection (Pre-Isthmian) was there sufficient running water for the passage of such forms.

(2) Of the still-water forms, 79% have passed over. These include all except the most cænogenetic genus of the *Æschninæ* (*Anax*), and the more recent genera of the *Libellulidæ* (*Diplacodes, Orthetrum, Hemicordulia*). Hence, for a very long period of time, probably during the whole of the Isthmian period, there was not sufficient running water on the isthmus to allow of the passage of running-water forms; but there was a good supply of still water, by means of which an abundant migration of still-water forms flourished. This conclusion will be seen to support, very strongly, Mr. Hedley's contention for a narrow Eastern Isthmus.

Let us now invert the problem, and classify our genera on the evidence before us. We may divide them into three groups:—

(1) *Pre-Isthmian genera.*

(*a*) Running-water forms that passed over in Pre-Isthmian times:—*Austroæschna*, *Æschna brevistyla* (this latter most probably passed *from* Tasmania *into* Victoria).

(*b*) Still-water forms that passed over during the period of "first elevation":—*Synthemis.*

(2) *Isthmian genera.*

(*a*) Running-water forms that failed to get across:—*Diphlebia, Argiolestes, Synlestes, Austrolestes cingulatus, Nososticta, Isosticta, Austrogomphus* (except *A. guérini*), *Metathemis*(?), *Hemicordulia australiæ.*

(*b*) Still-water forms that succeeded in crossing:—*Austrolestes* (*A. leda, A. annulosus, A. psyche, A. analis*), *Agrion, Ischnura, Austroagrion, Austrogomphus guérini, Procordulia, Nannophya, Austrothemis.*

3. *Post-Isthmian genera.*

Still-water forms that have failed to cross:—*Anax papuensis Hemicordulia tau* (very recent migration only), *Diplacodes, Orthetrum.*

The above classification, though it fails to give us any exact geological age in which to place the arrivals of the various genera into the area in question, is still of great value in exhibiting the *comparative* ages of the different groups, as shown by their arrivals at their southern limits of distribution.