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COMPETITIVE RELATIONSHIPS BETWEEN CERTAIN SPECIES OF FRESH-WATER TRICLADS

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(*With three Figures in the Text.*)

IF the influence of the bionomic environment on some particular species is to be investigated, it is first necessary to know what are the effects produced by changes in the physical environment. Otherwise phenomena which really depend on the physical environment may be wrongly described as bionomic effects.

Similarly, before considering the competitive relationships between different species of Triclad, it is necessary to know the limiting environmental factors for each, when they are *not* in competition with other species. Only in this way can an accurate idea of the extent of the effect of one on the other or others be obtained.

The species whose competitive relationships we have investigated are *Planaria montenegrina* Chickoff¹ with *Pl. gonocephala* Dugès, and *Pl. alpina* Dana with *Polycelis cornuta* Johnson.

The first case of competition which will be described is that of *Pl. montenegrina* with *Pl. gonocephala*. These animals were found in streams and springs in the western part of the Balkan Peninsula, in the district round Lake Ochrida, and in the Sorrento Peninsula in South Italy.

All the streams where the animals occurred were of the highland brook type (Carpenter, 1928 *b*), running swiftly down steeply sloping land. The bionomic environment was similar in all cases, and as it extended into regions where the temperature of the water was high enough to prevent the occurrence of these triclads, it could not therefore constitute a limiting factor. The physical environment, namely hard water flowing over a stony bottom, was also the same. In each stream system there was a gradual temperature increase from the source downwards. This gradient was in most cases uniform since the streams were unshaded.

¹ It is assumed in this paper that *Planaria teratophila* Steinmann found in South Italy is the same as *Planaria montenegrina* Chickoff which occurs in the Balkan Peninsula. This assumption appears to be justified, because it is difficult to find any morphological differences, and the ecological relationships are the same in the two cases.

Before considering *Pl. montenegrina* (= *Pl. teratophila*) and *Pl. gonocephala* in competition, it is necessary first to investigate the effects of temperature on the two species individually when they are not competing with each other.

Pl. montenegrina was found in undisputed possession of a stream near Agerola, on the steep southern side of the Sorrento Peninsula. Numerous springs formed the source of this stream in which the occurrence of the animal in relation to temperature is represented in Fig. 1. This map shows clearly that there is a sharply marked temperature limit at about 16.5° C.

It is interesting to note that the species is not found just above the mill. Here the water flowed through a wide shallow channel exposed to the sun where the rate of flow was less than in the natural stream with consequent heating up of the water.

Pl. montenegrina was present in many springs and streams in the West Balkans. It occurred in springs all of which were rheocrene with temperatures ranging from 6.6 to 14.2° C. Usually *Pl. gonocephala* was found lower down the streams, but in two places no competition was met with, at Piskepat, on the west shore of Lake Ochrida, and near Lin, also on the west shore of the same lake. The upper limiting temperatures in these two cases were 17 and 15.8° C.

It can therefore be said that *Pl. montenegrina* when not in competition with *Pl. gonocephala* has an upper temperature limit of 16–17° C.

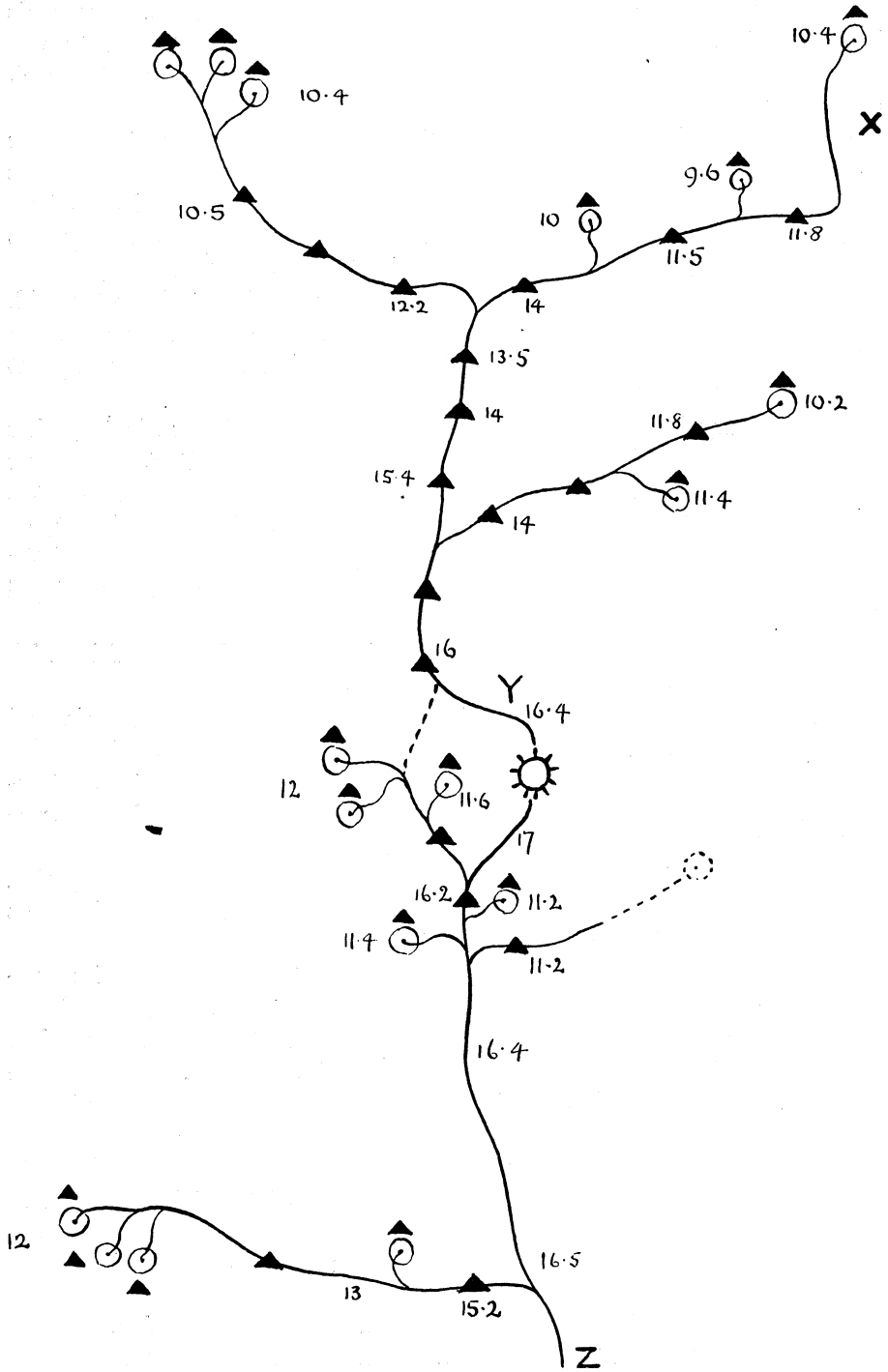
Pl. gonocephala was also found in springs and streams in Albania and southern Yugo-Slavia. When *Pl. montenegrina* is absent this species occurs right up to the spring head, where it was found in rheocrene conditions at temperatures of from 8.5 to 16.2° C. It was also present in two places in helocrene springs at temperatures of 18.6 and 19.2° C.

Pl. gonocephala is therefore capable, when not competing with other species, of extending from a region of temperature of over 20° C. to spring heads as cold as those occupied by *Pl. montenegrina*.

Having thus investigated the effect of temperature on each species separately, it is now possible to consider them in competition. They were found in the same stream system in many places in the West Balkans. Fig. 2 is a temperature-distribution map of a typical district (Dardha, near Korça in Albania). *Pl. montenegrina* was in sole possession of the spring heads and the upper parts of the streams, while *Pl. gonocephala* replaced it entirely in the lower parts. The temperature at which this occurred was from 13 to 14° C., and in all cases there was practically no intermixing of the two species.

In a typical stream therefore, conditions are:

From the spring head to 13–14° C. ...	<i>Pl. montenegrina</i> ,
From 13–14° C. to 21–23° C. <i>Pl. gonocephala</i> .



Lower down the stream at temperatures higher than 23° C. there were no planarians.

This limitation of the range of the two species by the presence of each other proves that interspecific competition is occurring; *Pl. montenegrina* is the more successful below 13–14° C., and *Pl. gonocephala* above this temperature.

It is interesting to note that, whereas the presence of *Pl. gonocephala* only limits the range of *Pl. montenegrina* by some 2 or 3° C., *Pl. montenegrina* causes a great limitation in the temperature range over which *Pl. gonocephala* is successful. This factor is of special importance in any consideration of the geographical distribution of the latter species.

The relationships just described are like those which Steinmann (1907), Zschokke (1900), Voigt (1892 and 1904) and others have shown to exist when *Pl. gonocephala* occurs together with *Pl. alpina* and *Pol. cornuta*.

These workers demonstrated that *Pl. alpina* occupies the spring head, and when occurring alone extends down the stream until limited by a temperature of from 14 to 15° C. Under similar conditions *Pol. cornuta* extends as far as 16–17° C., and *Pl. gonocephala* down to 23° C.

Where all three species live in the same stream it was shown that they formed a sequence along the stretch of water. *Pl. alpina* occurred from the spring head till replaced by *Pol. cornuta*, which in turn is supplanted by *Pl. gonocephala*.

The limiting temperature between *Pol. cornuta* and *Pl. gonocephala* is stated by various authors, and their results are in agreement that this occurs at some temperature very close to 15° C. However, when the limiting temperature between *Pl. alpina* and *Pol. cornuta* is quoted there is a much less exact agreement between the values obtained by the various workers. Steinmann gives it as 12° C., whereas Thienemann estimates it as 14.75° C.

The discrepancy in the latter case suggests that, whereas the relationships of *Pl. gonocephala* with *Pol. cornuta* are explicable simply in terms of temperature, the relations existing between *Pol. cornuta* and *Pl. alpina* themselves point to some factor other than temperature having an effect. This idea receives support in the experimental work of Frédéricq (1924), who studied the effect of raising the temperature of the medium in which the three species were kept. Under experimental conditions it was found that *Pl. gonocephala* can withstand a temperature of 32° C., while both *Pol. cornuta* and *Pl. alpina* can only tolerate a temperature of 27–28° C. The important point is that there is no de-

FIG. 1. Diagram-map of the distribution of *Pl. montenegrina* in the stream system found at Agerola (South Italy). The spoked circle represents a mill. Circles with dots in the centre represent springs. Black triangles denote the presence of the planarian. The numbers show the temperatures in ° C. At X a succession of steep waterfalls is the cause of the absence of *Pl. montenegrina*. At Y is the broad shallow channel referred to in the text. Below Z the stream was followed further until its temperature had risen to 19° C. At no point were planarians found. The temperatures were all taken during July 1930. The distance between the most distant source and the lowest point on the map was about 5 kilometres.

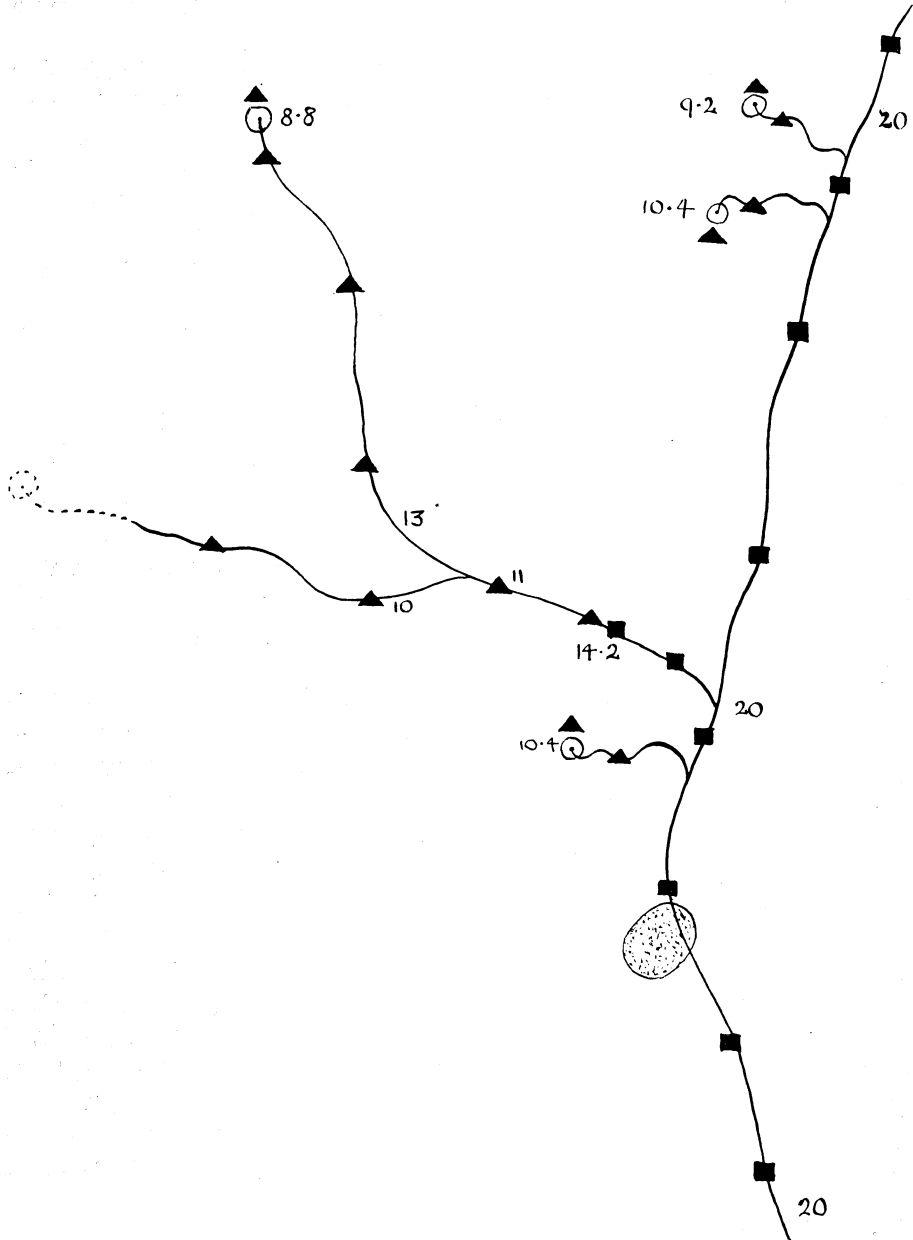


FIG. 2. Diagram-map of the distribution of *Pl. montenegrina* and *Pl. gonocephala* in the stream system at Dardha (near Korça in Albania). The dotted oval area represents the village of Dardha. Circles with dots in the centre represent springs. Black triangles denote the occurrence of *Pl. montenegrina*. Black squares denote the occurrence of *Pl. gonocephala*. The numbers show the temperatures in °C. All the temperatures were taken during August 1930.

tectable difference in the behaviour of *Pl. alpina* and *Pol. cornuta* towards temperature changes.

In the hope of obtaining information about the factor or factors other than temperature which affect the inter-relationships between these last two species, careful investigations of various streams, in which both animals occur, were made. Observations were made on streams in the Lake Maggiore district in North Italy, but the information derived from this source proved to be of far less interest and importance than that obtained recently from a study of the Cotswold area.

It was found that wherever the conditions are uniformly rheocrene a simple limiting temperature relationship exists, with *Pl. alpina* in sole possession of the spring head and extending down to 12·5–13·5° C. After this point *Pl. alpina* is replaced by *Pol. cornuta* which extends downstream as far as 16–17° C. This state of affairs was chiefly met with in North Italy, where the land slopes are much steeper than those of the Cotswolds, with the consequence that the rheocrene character is maintained beyond the temperature limit for *Pol. cornuta*.

In the Cotswolds, cold limnocrene springs are common. Under these conditions *Pol. cornuta* may be in complete possession of the spring head, or at least be present in equal numbers with *Pl. alpina*.

Thus, at Bibury there is a typical limnocrene spring with water welling up in a muddy basin containing numerous pieces of limestone. *Pol. cornuta* is in sole possession of the spring head at a temperature of 10° C., but, a few feet from the source, where the water begins to flow rapidly out of the pool, *Pol. cornuta* and *Pl. alpina* are to be found in equal numbers.

Similar conditions occur at Seven Springs (the source of the Thames) where the pool in which the springs well up is very large. It is interesting to note that in these semi-limnetic surroundings *Pol. nigra* and *Dendrocoelum lacteum* are also to be found at temperatures varying from 9·5 to 10·8° C. in different parts.

A specially interesting and illustrative case was found at Syrford. Fig. 3 is a map of the spring and stream system found there. Waters from two springs, marked *A* and *B*, join the main stream, which flows fairly slowly over a sandy or muddy bottom with scattered stones here and there, and in some places reeds.

In the stream itself, at temperatures below 13° C., *Pl. alpina* and *Pol. cornuta* were found in approximately equal numbers, the latter species, however, appearing to be slightly dominant. There was also a similar relationship between the two species in the spring *B*, which is limnocrene in character and has a level scarcely above that of the main stream, so that the flow is very gentle.

The position of the spring *A* is, however, quite different. It is situated considerably above the main stream and pours water down a steep slope over

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which the rate of flow is rapid. *Pl. alpina* is here in exclusive possession of the spring head and that part of the course to the main stream where the water is flowing swiftly down the slope. The two springs, which both have the same temperature (9.5° C.), are situated not more than 20 yards apart.

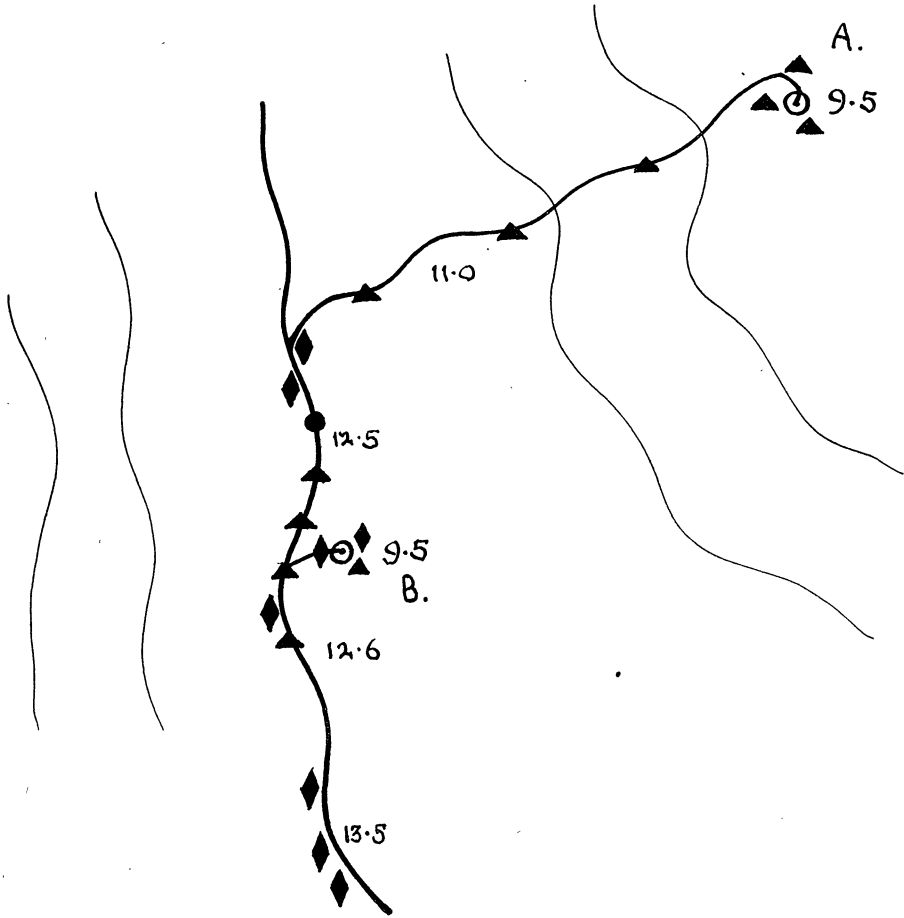


FIG. 3. Diagram-map of the distribution of *Pl. alpina* and *Pol. cornuta* in the stream system at Syrford (in the Cotswolds, England). For description see text. Circles with dots in the centre represent springs. Black triangles denote the occurrence of *Pl. alpina*. Black diamonds denote the occurrence of *Pol. cornuta*. Black circles denote the occurrence of *Pol. nigra*. The numbers show the temperatures in ° C. All temperatures were taken during the early part of September 1930.

From this evidence it is apparent that the rate of flow of the current, as well as the temperature, is a very important factor in determining the success and efficiency of *Pl. alpina* and *Pol. cornuta* when in competition with each other.

In cold rheocene springs *Pl. alpina* will be in possession of the spring and stream head, while in cold limnocene springs both *Pl. alpina* and *Pol. cornuta* may either occur in equal numbers, or where there is practically no current until the water overflows the basin in which the spring arises, *Pl. alpina* may be excluded from the basin by *Pol. cornuta* and be found only where the water is flowing away.

SUMMARY.

1. When *Pl. montenegrina* (= *Pl. teratophila*) and *Pl. gonocephala* occur in competition with each other, *temperature* is the factor which governs the relative success and efficiency of the two species. *Pl. montenegrina* is the more successful at temperatures below 13–14° C. Above these temperatures *Pl. gonocephala* is the more efficient form.

2. When *Pl. alpina* is in competition with *Pol. cornuta*, the governing factor is not so much temperature as the *rate of flow* of the water. At temperatures in the neighbourhood of 9° C. *Pl. alpina* is successful in rheocene conditions, but *Pol. cornuta* dominates in limnocene conditions.

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