Predators and planariid competitors of the triclad *Phagocata vitta* (Dugés)

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Abstract

When *Phagocata vitta*, *Crenobia alpina* and *Polycelis felina* were exposed separately to each of seventeen potential invertebrate predators in the laboratory, only two stonefly species, *Dinocras cephalotes* and *Perlodes microcephala*, fed on the three triclad species, whilst the trichopteran *Rhyacophila dorsalis* ate the last two triclads. On exposing pairs of triclad species to *D. cephalotes*, significantly more *P. felina* than *Ph. vitta* were consumed, whereas similar numbers were eaten in each of the other two triclad combinations. Cannibalism and interspecific predation by triclad species were not observed. It is concluded that predation is unlikely to have a major influence in determining the observed distribution and abundance of triclad species in a Welsh study stream which harbours low numbers of effective predators.

The de Wit model of competition was used to examine the competitive relationships between *Ph. vitta*, and *C. alpina* and *P. felina*, using chironomids or tubificid worms as food. In mixed cultures of *Ph. vitta* and *P. felina* fed on tubificids a stable equilibrium existed within the range of relative densities used in the experiments, whereas *Ph. vitta* was competitively superior to *C. alpina* in cultures fed on each of the food types, and to *P. felina* fed on chironomids. However, in theory, an equilibrium could occur when 10 or 6–7 times as many *Ph. vitta* as *P. felina* and *C. alpina* respectively are in the culture, when intraspecific rather than interspecific competition would become more important. Where the three triclad species coexist in the Welsh study stream, they are in similar numbers. This could imply that food is not limiting, with no consequent interspecific competition, or that the laboratory experiments were too simplistic to allow any interpretation of the field situation.

Introduction

The intensity of predation on triclad populations inhabiting the stony littoral zone of British lakes is too low to exert any major effect on their abundances (Davies & Reynoldson, 1971; Reynoldson, 1983). However, in small weedy lentic habitats, predation can greatly reduce or eliminate triclad populations (Davies, 1969). In British streams, it has proved difficult to determine to what extent predation contributes to triclad mortality, but Wright (1975) concluded from studies on streams in North Wales that, in certain situations, predators influenced the micro-distribution of triclads and depressed their numbers.

Interspecific competition for food plays a major role in determining the abundance and distribution of British lake-dwelling triclad species (Reynoldson, 1966, 1983), and there is some evidence that it may occur between the two british stream-dwelling triclads *Crenobia alpina* (Dana) and *Polycelis felina* (Dalyell) (Lock & Reynoldson, 1976).

This paper presents the results of a laboratory study of the predators and competitors of *Phagocata vitta* (Dugès), which formed part of a major investigation of the ecology of this triclad in a small stream, the Anafon 1, a tributary of the Afon Anafon in Gwynedd, North Wales (Grid Ref. SH 679710) (Armitage, 1988). Hitherto, studies on British stream-dwelling triclads have focused mainly on *C. alpina* and *P. felina* (e.g. Wright, 1972, 1974, 1975; Lock, 1972, 1975; Lock & Reynoldson, 1976).

Methods

Predators

The following experiments were conducted at 10 °C with a photoperiod of 12 hrL : 12 hrD. Experimental and control dishes were filled with 500 ml of stream water from the field-study site. Control dishes, containing triclads only, matched the number of experimental dishes, containing predators and triclads. Unless otherwise stated, triclads of 5–7 mm in length were used.

Determination of potential predators

Ph. vitta was exposed to seventeen potential invertebrate predators which occurred in the field-study stream Anafon 1. Opportunity was also taken of studying predation of *C. alpina* and *P. felina* which co-occurred with *Ph. vitta* in the study stream. Each experimental dish contained 10 triclads and 5 predators of the species under consideration. Five replicates of each predator and triclad combination were used. After one week, the number of surviving triclads was noted.

Choice of triclad species by Dinocras cephalotes

Paris of triclad species were exposed simulta-neously in glass dishes to the stonefly nymph *Dinocras cephalotes* to determine if there was any preference for a particular species. Each dish contained 3 *D. cephalotes* (25 mm in length) and 4 triclads (7 mm in length) of each of the triclad species being offered. For each regime, 10 replicates were used and dishes were inspected daily, over 10 days, when any triclads eaten were noted and replaced.

Cannibalism and interspecific predation by triclads

Cannibalism was investigated using triclads of a particular species which had been starved for 3 weeks prior to the experiment. For each species, 10 triclads were placed in each of 10 dishes; these experimental triclads were not fed during the experiment. Each experimental series was matched by ten control dishes, with each dish containing 10 triclads which were fed daily with tubificid worms. The experiment lasted 10 days with dishes examined daily when any missing triclads were noted and replaced.

Interspecific predation was examined using dishes containing 5 triclads of each of two species, in every combination of *Ph. vitta*, *C. alpina* and *P. felina*. Ten replicates were used for each combination, together with 10 controls containing each species on its own. Again, over a period of 10 days, the number of triclads which disappeared daily was noted and replaced.

Competitors

The de Wit (1960, 1961, 1971) model of competition was used to examine the competitive relationships between *Ph. vitta*, and *C. alpina* and *P. felina*. This model was used successfully by Sigurjonsdottir & Reynoldson (1977) to investigate relationships between the lake-dwelling triclads *Polycelis tenuis*, *Dugesia polychroa* and *Dendrocoelum lacteum*. In the use of the model, the overall density of the animals is kept constant, whilst the relative proportions of the two competing species are varied in the mixture in a replacement series. The biomass of each species is initially recorded and is compared with the output of biomass of each species after competition has taken place. The log of the input ratio of the

biomasses of the two competing species is plotted against the corresponding log of the output ratio, and a regression line is calculated. The line obtained can then be compared with the theoretical equilibrium ratio line, which has a gradient of 1 and passes through the origin. The equilibrium line corresponds to the situation where the input biomass ratios are equal to the output biomass ratios, and this corresponds to a situation of stable co-existence. Four positions of the calculated regression lines are possible, relative to the equilibrium line, and these correspond to the four possible outcomes of competition predicted by the Lotka-Volterra model of interspecific competition (see Begon, Harper & Townsend, 1986).

Experimental triclads were obtained from small streams, adjacent to the field study stream, flowing into the Afon Anafon, North Wales (Armitage, 1988). Chironomid larvae and tubificid worms were used as food in the experiment because these were the main prey taxa of the three triclad species in the field (Armitage, 1988; Armitage & Young, 1990). Initially, the feeding rates of the triclad species upon the two prey types were determined to allow a situation of food limitation, and consequent competition, to be generated in the experiments (Armitage, 1988). Triclads were kept in glass dishes, 15 cm in diameter and containing 500 ml of stream water, and maintained at 10 °C, an optimum temperature for the three species, with a photoperiod of 12 hrsL : 12 hrsD. Experimental regimes were established, pairing *Ph. Vitta* with *C. alpina* or *P. felina*, and these were fed with chironomids or tubificids. For each combination of triclad species and single food type, six density combinations were used to form the following replacement series:

species 1 – 10   8   6   4   2   0
species 2 –   0   2   4   6   8   10

Due to the large number of dishes and triclads required and the time consuming maintainance of the cultures, only two replicates of each density combination were used.

The triclads were fed at weekly intervals, with 3 chironomids (6–10 mm in length) or 5 tubificids (about 15 mm in length) added to each dish. The lengths of the triclads were measured initially,

when a similar length range (4–8 mm) was used for each triclad species, and subsequently at fortnightly intervals over a period of 14 weeks. For each triclad species, all lengths were subsequently converted into weights using regression equations (see Armitage, 1988).

Results

Determination of potential predators
Very few of the potential invertebrate predators preyed on the triclad species (Table 1). Only the two stonefly species, *Dinocras cephalotes* and *Perlodes microcephala*, ate all three species of triclads, whilst the trichopteran *Rhyacophila dorsalis* fed on *C. alpina* and *P. felina*. No mortality occurred in the controls.

Choice of triclad species by Dinocras cephalotes
Using t-test analysis, no significant difference $(P > 0.05)$ was found between the numbers of each triclad species eaten when *Ph. vitta* and *C. alpina* or *P. felina* and *C. alpina* were offered to the stonefly, but significantly $(P < 0.05)$ more *P. felina* were eaten when offered in combination with *Ph. vitta* (Table 2). No deaths were recorded in the controls.

Cannibalism and interspecific predation by triclads
There was no evidence of cannibalism, with no deaths recorded in either the experimental or control dishes. Also, there was no evidence for interspecific predation; again, no triclads died in the experimental or control dishes.

Competitors
Regression analysis was applied to the input-output biomass ratio data, but no other statistical analysis was possible due to the small number of replicates used. However, in most cases the two replicates for a particular species pair at a particular relative density showed similar trends. Unfortunately, when *Ph. vitta* and *C. alpina* were placed in competition, one replicate (4 Ph.v : 6 C.a.) fed on chironomids and one replicate (8 Ph.v. : 2 C.a.) fed on tubificids, died

Table 1. Triclad species eaten (+) or not eaten (−) when exposed to potential predators.

Potential predators	Triclads		
	Phagocata vitta	*Polycelis felina*	*Crenobia alpina*
Amphipoda			
Gammarus pulex (L.)	−	−	−
Triochoptera			
Hydropsyche siltalai Dohler	−	−	−
Philopotamus montanus (Donov.)	−	−	−
Rhyacophila dorsalis (Curtis)	−	−	−
Tinodes dives (Pictet)	−	−	−
Agapetes fuscipes Curtis	−	−	−
Limnephilidae (unident.)	−	−	−
Plecoptera			
Dinocras cephalotes (Curtis)	+	+	+
Perla bipunctata Pictet	−	−	−
Chloroperla torrentium (Pictet)	−	−	−
Isoperla grammatica (Poda)	−	−	−
Perlodes microcephala (Pictet)	+	+	+
Coleoptera			
Elmis aenea (Mull.)	−	−	−
Diptera			
Chironomidae (unident.)	−	−	−
Pedicia sp.	−	−	−
Ceratopogonidae (unident.)	−	−	−

inexplicably. 'Growth' rates were calculated as, (biomass at time *t* − original biomass)/biomass at time *t*, but these are not shown in the interests of space. They revealed either positive growth or shrinkage during the experiments, a phenomenon also obtained by Sigurjonsdottir & Reynoldson (1977). In the present study monocultures showed positive growth, with one exceptional replicate of *P. felina* fed on chironomids. The very small number of cocoons produced by *C. alpina* during

the experiment were ignored. Some fission by *P. felina* occurred and the new individuals produced were left in the dishes, as they comprised a component of the biomass. This may have led to a source of error as more mouths were feeding on the food supplied, but the problem was insurmountable.

Ph. vitta vs P. felina

Input/output biomass ratios and regression lines are shown in Fig. 1. With chironomids as food, all plotted points are above the equilibrium line, implying that the biomass of *Ph. vitta* is increasing in relation to that of *P. felina*, and that the former species is competitively superior to the latter (Fig. 1a). However, the regression line for the input-output ratio does converge slowly with the equilibrium line suggesting, in theory, that co-existence could occur when ten times as many *Ph. vitta* as *P. felina* are in the mixed culture. Unfortunately, the lack of replication does not allow any estimate of the probability that con-

Table 2. Mean number of triclads eaten by *Dinocras cephalotes* when two triclad species were offered simultaneously.

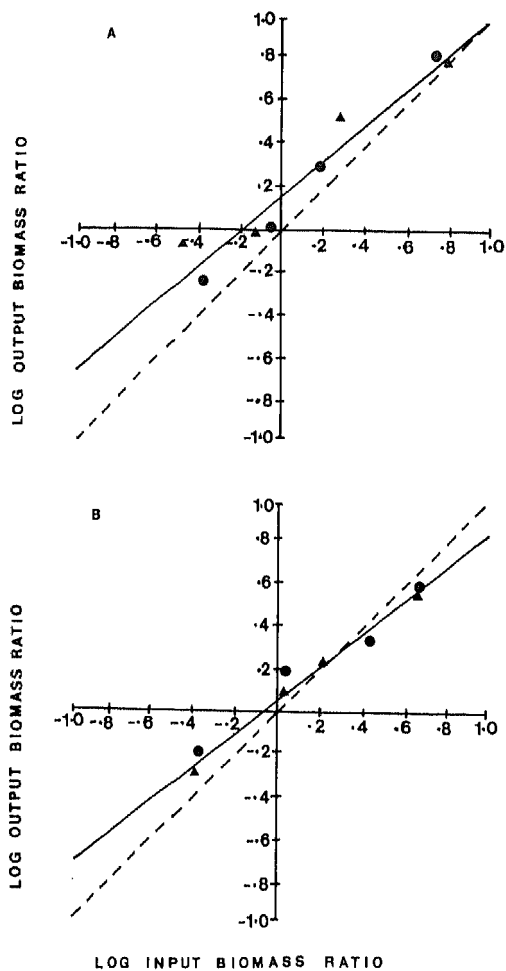| Triclad species combination	Mean number of triclads eaten		
	Phagocata vitta	*Polycelis felina*	*Crenobia alipna*
Ph. vitta + C. alpina	6.4	−	6.0
Ph. vitta + P. felina	5.7	7.0	−
C. alpina + P. felina	−	7.3	5.8

Fig. 1. Regression plots of *Phagocata vitta/Polycelis felina* input ratios against output ratios, when fed on (a) chironomid larvae and (b) tubificid worms. Dots and triangles show the data separately for each replicate. Broken line indicates the equilibrium condition.

Fig. 2. Course lines of *Phagocata vitta* and *Polycelis felina* maintained together and fed on (a) chironomid larvae and (b) tubificid worms. Broken and continuous lines refer to separate replicates, with the numerical ratio of *Ph.v.* : *P.f.* indicated at the end of the lines.

vergence is real with a slope significantly less than unity. The course lines for the biomass ratio of *Ph. vitta/P. felina* reveal a general trend for increase as the experiment proceeded (Fig. 2a). Variability between the replicates is low, with the exception of one of the replicates of the 6:4 regime, where *Ph. vitta* gains dramatically over *P. felina*. The growth curves (not shown) for each species indicated that *Ph. vitta* gained in biomass in all density mixtures, whereas *P. felina* shrank in many. Overall, it appeared that *Ph. vitta* was outcompeting *P. felina* when chironomids were
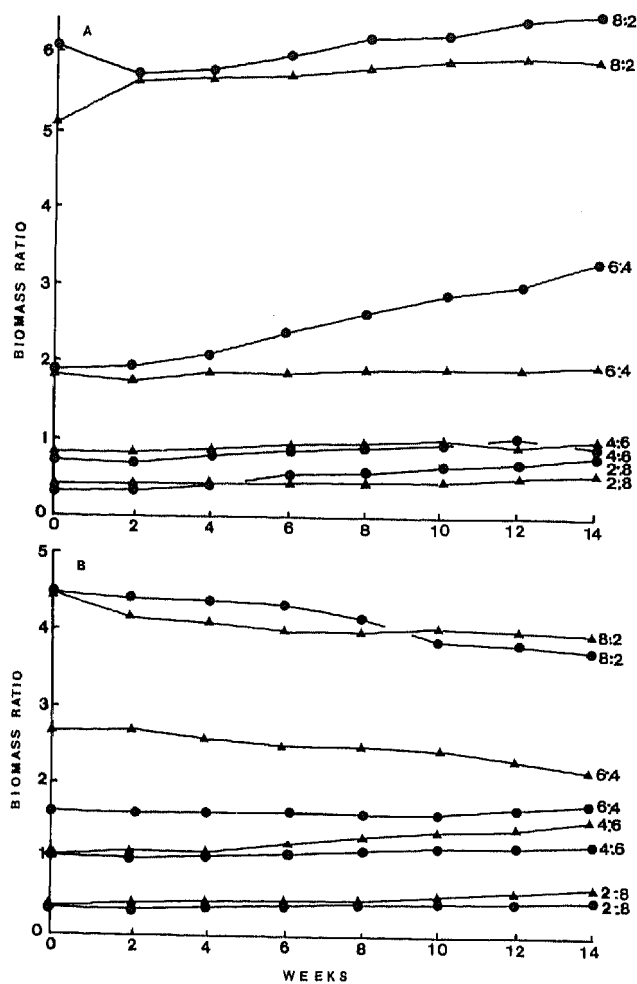
supplied as food, tending to increase in biomass at their expense.

With tubificids as food, the plotted values of input/output biomass ratios were found on either side of the equilibrium line (Fig. 1b). The calculated regression line intercepts the equilibrium line when twice as many *Ph. vitta* as *P. felina* were in the culture, corresponding to a stable equilibrium. The course lines also show this tendancy towards equilibrium (Fig. 2b). When *Ph. vitta* was in lower proportions, the trend was for a gradual increase in the *Ph. vitta/P. felina* biomass ratio,

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whilst, when the proportion of *Ph. vitta* was initially high, the tendancy was for a gradual decline. Growth curves for each species revealed *Ph. vitta* to perform slightly better than *P. felina*.

Ph. vitta vs C. alpina

The input/output biomass regression lines are shown in Fig. 3, and there is considerable similarity between the regimes fed on chironomids and tubificids. The regression lines mostly remain above the equilibrium line, which would imply a strong competitive performance by *Ph. vitta*. However, the regression and equilibrium lines do converge and intercept at a point where there are
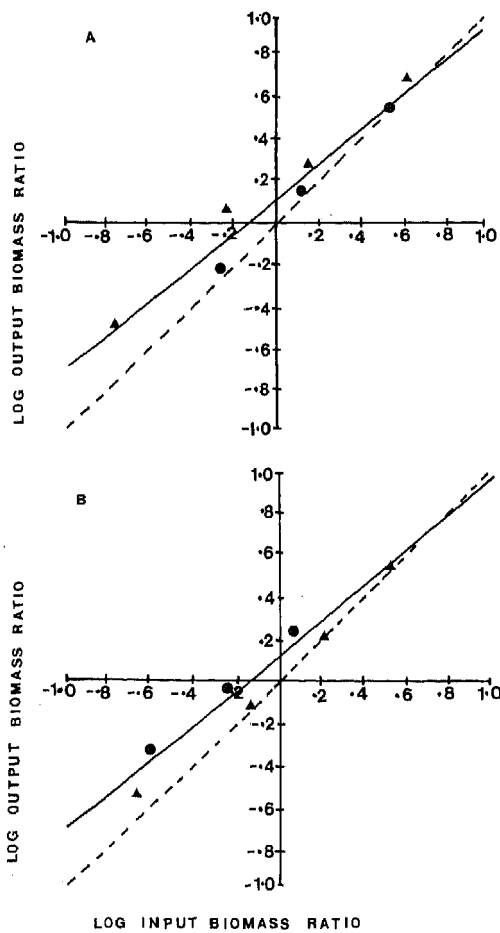
six times or seven times, in the case of the chironomid and tubificid regimes respectively, as many *Ph. vitta* as *C. alpina* in the mixed culture, indicating a theoretically stable equilibrium situation.

For each food regime, the course lines showed a strong similarity between the replicates and a tendancy for a slight increase in the biomass ratio as the experiments proceeded (Fig. 4). Growth curves (not shown) indicated shrinkage in some mixed cultures for both *Ph. vitta* and *C. alpina*, but particularly for the latter when in high proportions in the initial input mixture.

Discussion

The present laboratory results on the predation of triclads are in broad agreement with the findings

Fig. 3. Regression plots of *Phagocata vitta/Crenobia alpina* input ratios against output ratios, when fed on (a) chironomid larvae and (b) tubificid worms. Dots and triangles show the data separately for each replicate. Broken line indicates the equilibrium condition.
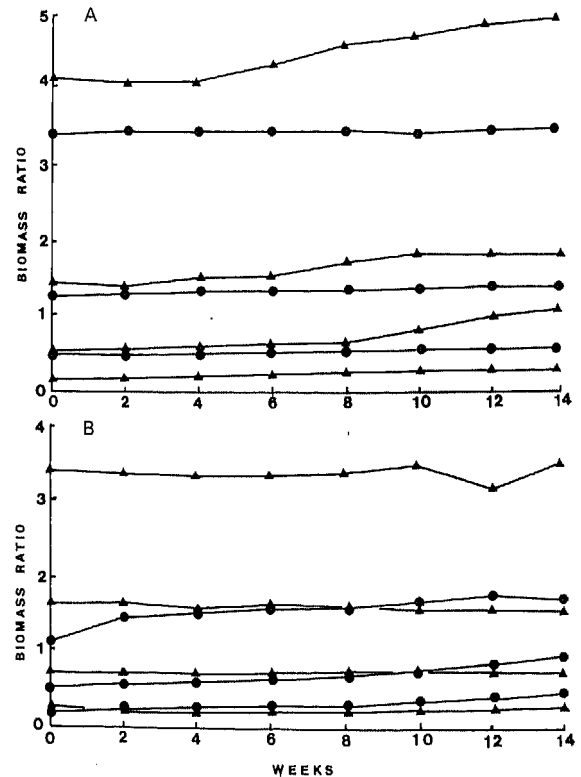

Fig. 4. Course lines of *Phagocata vitta* and *Crenobia alpina* maintained together and fed on (a) chironomid larvae and (b) tubificid worms. Broken and continuous lines refer to separate replicates, with the numerical ratio of *Ph.v.* : *C.a.* indicated at the end of the lines.

of Wright (1975), who used a serological method to identify triclad remains in the gut of stream-collected potential invertebrate predators; this approach could not be used in the present study due to the low number of potential predators in the study stream. Wright found that *Dinocras cephalotes, Perlodes microcephala, Rhyacophala* sp. and *Isoperla grammatica*, in order of decreasing importance, had eaten triclads. Unfortunately, his anti-triclad serum did not distinguish between the triclad species.

Of the three invertebrate species which fed upon triclads in the present laboratory investigation, only the stonefly *Dinocras cephalotes* occurred in any numbers in the study stream, Anafon 1 (Armitage, 1988). During the field study, samples of invertebrates were taken from the stream at 11 sites, site 1 being furthest upstream and site 11 furthest downstream near its confluence with the Afon Anafon. Analysis using the Spearman Rank Correlation coefficient revealed no significant correlation ($P > 0.05$) in the abundance of *D. cephalotes* and *Phagocata vitta* at the 11 sites. In the laboratory, though *D. cephalotes* did feed on the three triclad species, it ate a slightly greater number of *Polycelis felina*. Interestingly, *P. felina* was absent from the stream below site 6 where large numbers of *D. cephalotes* were present, which suggests that predation may have been implicated in depleting this triclad's numbers. Earlier, Wright (1975) suggested that, in some circumstances, predation by *D. cephalotes* might effect the microdistribution of triclads and depress their abundance. However, in the present investigation, it is concluded that, with the possible exception of *D. cephalotes* contributing to *P. felina* mortality, it seems unlikely that predation is a major factor determining the abundance and distribution pattern of the triclad species in the study stream.

A serological investigation of the diets of *Ph. vitta, C. alpina* and *P. felina* in the field indicated considerable food overlap, with three major food taxa, oligochaetes, chironomids and, to a lesser extent, *Gammarus*, being eaten (Armitage, 1988; Armitage & Young, 1990).

Thus, where the three triclad species coexist in the field it seems likely that some degree of competition would occur if food is in short supply. An examination of the abundance and distribution of the triclads in the study stream, Anafon 1, revealed that the three species coexisted and had similar, peak abundances at a particular site, station 6 (see Armitage, 1988).

In the current laboratory experiments, in cultures of *Ph. vitta* and *P. felina* fed on tubificids, a stable equilibrium was obtained within the range of relative densities used. In the other mixed cultures, *Ph. vitta* appeared to perform well at the expense of both *C. alpina* and *P. felina*. However, in theory, coexistence between the two competing species was predicted as being possible when may more *Ph. vitta* than their competitors were present in the dishes. In this situation, it is probable that intraspecific competition would be limiting *Ph. vitta* and would be more severe than interspecific competition. Further increase in the biomass of the triclad would therefore be checked, allowing any remaining competitors to persist in small numbers.

The fact that this experimental situation, i.e. coexistence with *Ph. vitta* in numerical superiority, was not observed in the Anafon 1 study stream, where, as stated above, similar numbers of all three triclad species coexisted, could imply that food was not limiting. Some other factor(s), apart from competition, for example, disturbance (Townsend, 1989), may be limiting the abundance and distribution of *Ph. vitta* and the other two triclad species. However, the simplistic nature of the experiments should be borne in mind. Only one prey type was used in each regime and there was no opportunity for diversification of the diet of the triclads under conditions of food shortage and competition. Furthermore, in the field the three triclad species would be interacting simultaneously rather than in species pairs as used in the experiments, and this may prevent, in some undetermined way, the domination of a single species.

The role of other environmental factors in effecting the distribution and population dynamics of *Ph. vitta* will be discussed elsewhere.

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