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CONTRIBUTIONS TO THE BIOLOGY OF THE DOMESTIC LAMPYRIDAE LAMPYRIS NOCTILUCA GEOFFR. AND PHAUSIS SPLENDIDULA LEC. AND EXPERIMENTAL ANALYSIS OF THEIR PREDATORY AND SEXUAL BEHAVIOR

[Following is a translation of an article by Hans Helmut Schwalb in the German-language periodical Zoologisches Jahrbuch (Zoological Annual), Vol 88, No 4, 1961, pages 399-550.]

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A. Introduction, Survey of the Literature, and Statement of the Problem

The fireflies are among the best known of our native fauna, so that it is understandable that the scientific literature concerning them is very extensive. A good survey of the European and non-European literature is given by Harvey [53,55; here and below, the numbers in square brackets after the author's name indicate the number in the bibliography at the end of this article] in his two compilational works on bioluminescence. The European literature breaks off after the first quarter of this century, having reached its peak in the first two decades. It concerned itself chiefly with the phenomenon of luminescence and limited itself in Europe particularly to anatomy and histology (Bongardt [9], Vogel [127,128,129,130], M. Schultze [116], Wielowiejski [140]) and to the physiology of the luminous organs (Bongardt [8,9], Kölliker [69], Kuhnt [70], Macaire [76], Perkins [101], Owsjanikow [100], Weber [136], Weitlaner [137,138], Wielowiejski [140]). There was also some study of the morphology of the larvae and imagines (Acloque [1], Bongardt [9], Höllrigl [62], Knauer [68], Maille [77], Olivier [96,97,99], Verhoeff [126], Vogel [127,129,131], Weber [135,136], Wielowiejski [140]), but biological observations or even experiments and also ethological notes are rare, very scattered, and often contradictory, being based only on accidental observation or on teleological speculation (e.g. Acloque [1], Bongardt [8,9], von Bronsart [13], Czepa [31,32], Dieckhoff [34], Emery [37,38], Höllrigl [62], Macaire [76], Morley [94], Newport [95], Olivier [96,97], Verhoeff [126], Vogel [127,129], Weber [136], Weitlaner [137], Wielowiejski [140]). Olivier [96], who in his day brought out the first compilational works, writes, "De même, leurs moeurs ont été également peu observées; les documents relatifs à leur genre de vie et à leur éthologie font à peu près entièrement défaut et, dans beaucoup de genres, on ne connaît que les individus mâles." ["In the same way their habits have likewise been little observed; documents dealing with their mode of life and their ethology are almost entirely lacking, and in many genera we are acquainted only with male specimens."] He appeals to the entomologists and holds out a promise of rich discoveries. Similar statements were made by Mangold (1910) and Verhoeff [126] and by the Americans Buck [23], Hess [58], Mast [82], McDermott [84], and others.

In the narrower field of my investigations (sexual behavior) the non-European literature (and in part the southern European, as concerns the *Luciola* species) must be considered apart (cf. Chapter D I). American research into the

problem of luminescence has been conducted along many lines and is still continuing. The morphology, anatomy, and histology of the luminous organs of the species found there have been treated by Brown and King [14], Buck [23], Geipel [44], Haddon [51], Harvey [52], Hess [58], and the physiology and in particular the biochemistry of the process of luminescence have so far been studied almost solely by American authors (Alexander [3], Brown and King [14], Buck [20,22,23], Dubois [35], Emerson [see Note 1], Lund [75], Malouf [see Note 1], Snell [120], Snyder [121]). Other American works concern themselves more or less intensively with the biological side of luminescence and its connection with sexual behavior (Buck [19,21], Hess [58], Hutson [63], Mast [82], McDermott [83 to 88], Williams [see Note 2].

[Note1] For exact reference see Harvey [55].

[Note2] Williams, F.X., "Notes on the Life History of Some North-American Lampyridae," Journal of the New York Entomological Society, Vol 25, 1917, pages 11-33. This contribution was unfortunately not available to me.

For our native lampyridae there are as yet no experimentally proved findings on the significance of the capacity of luminescence for the sexual behavior. My studies have therefore dealt with the following questions:

1. Normal sexual behavior of Lampyris and Phausis in the open,
2. Qualitative and quantitative analysis of the sexual stimuli of the two species,
3. Physical nature of the light emitted by the two species,
4. Decoy experiments with artificial sources of light,
5. Qualities of Lampyris and Phausis light that distinguish the two species, and
6. Comparison with the differing mechanisms of luminescence of the southern European Luciola species and the American lampyridae thus far known.

I also set myself the task, not successfully attempted previously, of raising the two native species of fireflies from egg to imago. In the course of my experimental studies I was also able to fill in various gaps in our knowledge of the developmental cycle of the animals and to make unexpected observations on the biology of the larvae.

I should like to express here my profound gratitude to my revered teacher, Prof.Dr. F. Schaller, for suggesting the subject and for his tireless readiness to help.

I also thank Prof.Dr. Mislin for his interest in the work and for providing the place to work.

For repeated assistance in capturing the specimens, and for accompanying and assisting me in my nocturnal capturing excursions and my experiments in the open I owe a debt of thanks to my friends and colleagues.

B. Materials and Methods

Since of the three native species of fireflies Phosphaenus hemipterus is extremely rare, I worked only with Lampyris noctiluca and Phausis splendidula, which I collected chiefly in the area around Mainz and in the vicinity of my home town of Hettenleidelheim on the northeast edge of the Palatine forest. The animals could be captured only at night, when they glowed, in certain biotopes. The larvae luminesce at very capricious times, and for that reason were especially hard to find (often I found only one or two a night). Except for the winter months, however, they can luminesce almost the year round. To capture the larvae it is necessary to resort to practices determined by habits of luminescence peculiar to the species (cf. pages 47 ff. and Chapter C II 1). Capture of the imagines is possible only during a very brief season of the year and then only from the beginning of darkness until toward midnight (two or three hours). They often show up suddenly in a biotope and are quickly gone again (Chapter D I 1). Besides that the Lampyris males, which were so important in my experiments, do not visibly luminesce. All this may have contributed to the previous lack of biological studies.

For nourishment, culture conditions, and the rearing of the larvae from the egg, cf. Chapter C.

The short-lived imagines were kept in large petri dishes (height 12 cm, diameter 30 cm) under largely natural habitat conditions (see Chapter C I), separated by sex.

In view of the numerous and varied methods of study employed in the course of the work it is best to discuss them separately in the individual chapters. In principle all laboratory experiments were preceded or accompanied by extensive out-of-doors observations in the natural environment. All investigations were carried out at night or in the late evening hours — unless otherwise determined by the nature of the experiment — in order to do justice as far as possible to the natural conditions of activity of the animals (cf. Chapter C III 1 and D I 1,2).

C. Ecology, Developmental Cycle, Larval Biology

I. Ecology

A rapid glance at the brief remarks not uncommonly inserted in the literature concerning the localities where fireflies are found (Bongardt, Emery, Hess, Höllrigl, Knauer, Macaire, Newport, Verhoeff, Vogel), both European and non-

European species, indicates that they live chiefly in damp places: in wet meadows, along the banks of brooks and rivers, in bushes, at the edge of woods, etc. By a comparison of various biotopes it is our intention here not only to work out their common and their divergent characteristics, but more especially to consider whether the two species inhabit separate biotopes or whether they occur together and why.

1. Biotope

Of the 18 separate biotopes that became known to me, 12 were under constant observation, while I only visited the others occasionally. These 12 habitats are situated in areas divergent both in landscape and in geology.

Eleven are in the immediate zone of influence of woods or a woods-like environment (park grounds, cemeteries, patches of woodland among the fields, and the like); only one consists of treeless and almost bushless terrain, namely of slopes covered with rank grass broken by cultivated ground, with only scattered fruit trees, blackthorns, and dog-rose bushes (biotope B). It is striking that none of the habitats known to me shows even the slightest growth of conifers, but — if anything — deciduous woods or more or less light bushes. Nine have direct contact with open water, either standing or flowing; the rest have such a high groundwater level sometimes that the areas frequently become marshy. A comparison of the floristic inventory will give further information about the physical appearance of their habitats and about special peculiarities in their colonization. The following biotopes were occupied in August (1958):

Figure 1.

Biotope A (Figure 1)

In a wooded valley beside a pond.

1. Subsoil: partly exposed sandy loam (Lower Permian sandstone);

2. Soil: peat, raw humus, moderate to dense grass (root) mat;

3. Herb stratum: grasses, ferns, oxalis, equisetum; commonly also Rumex acetosa, Gallum aparine, Lactuca spec., Stellaria media, Urtica dioeca.

4. Brushwood stratum: predominant: Rubus fruticosus and idaeus, Populus nigra, Robinia, Quercus robur, Fagus silvatica; scattered: Evonymus, Betula verrucosa, Corylus avellana. — The brushwood stratum is very strongly marked. Representatives of the tree stratum occur only as bushes. The tree stratum is thus lacking.

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GRAPHIC NOT REPRODUCIBLE

Figure 2.

Biotope B (Figure 2)

Slopes in open cultivated land near the bank of a small stream.

1. Subsoil: limestone and clayey soil of limestone content, covered with a topsoil layer.

2. Surface layer: extremely thick mat of grass roots and stems, with only occasional patches of moss.

3. Herb stratum: almost exclusively grasses up to one meter high: Achillea millefolium, Cichorium intybus, Senecio varieties, Daucus, Chenopodium varieties.

4. Brushwood and tree stratum: Rosa canina, fruit trees (pear, apple, plum).

Biotope C (Figure 3)

Figure 3.

In the upper end of a small watercourse.

1. Subsoil: variegated sandstone and a thin weathered layer of same, completely covered with the topsoil.

2. Surface layer: very thick, mosses, 5-10 cm raw humus, dense mat of grass roots, etc.

3. Herb stratum very weakly developed because of extremely dense brushwood stratum. Predominant: gramineae, juncaceae, polypodiaceae, oxalis, teucrium, Fragaria vesca, Scorodonia; scattered: Viola canina, Scrophularia spec., Stachys spec.

4. Brushwood stratum: dense stand about 2 m high of Carpinus betulus, with scattered Fagus silvatica, Quercus robur, Corylus avellana, Alnus, Rubus fruticosus and idaeus, Populus nigra, Betula verrucosa, Salix caprea; at the edge of the biotope a thick stand about 5-15 m high of spruce, pine, and fir; no marked tree stratum in the biotope itself.

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Figure 4.

Biotope D (Figure 4)

On a small woodland stream, downstream from biotope C.

1. Subsoil: as in C.

2. Surface layer: as in C.

3. Herb stratum as in C, with the addition of melilot (in abundance), Plantago lanceolata, Taraxacum spec., Urtica dioeca, Valeriana off., Melampyrum spec.

4. Brushwood stratum: predominant: Corylus avellana, Quercus robur, Salix caprea; scattered: Carpinus betulus, Fagus silvatica, Betula verrucosa, Prunus avium, Bryonia alba, Fraxinus excelsior, Alnus, Prunus spinosa, Viburnum, Acer pseudoplatanus, Evonymus, Rosa canina. No tree stratum.

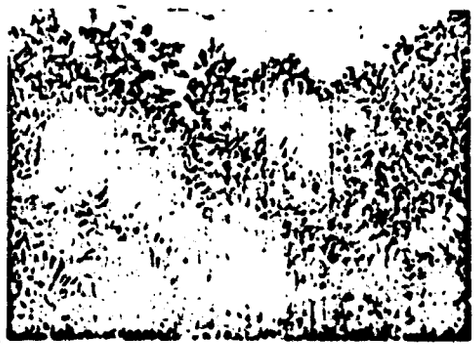

Figure 5.

Biotope E (Figure 5)

Extensive covert near a wood and surrounded by an artificial groundwater lake.

1. Subsoil: clayey sand (so-called "luting sand"), not exposed.

2. Surface layer: raw humus 5-10 cm thick under a stand of pedunculate oak of bush height. Toward the edge of the field dense grassroots and stalks form a continuous ground cover; little moss.

3. Herb stratum: in dense oak and hedge terrain, completely lacking; otherwise grasses predominate. Scattered: melilot, Plantago species, Stellaria media, Epilobium silvaticum, Urtica dioeca, Juncaceae, Aspidium filix mas, Silene inflata.

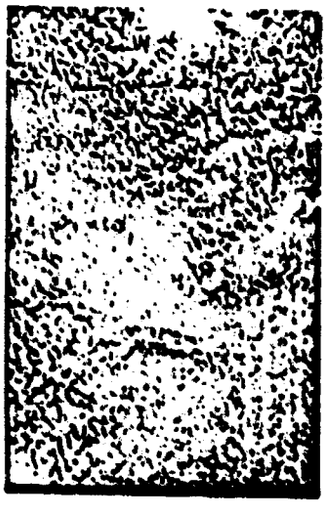

Figure 6.

4. Brushwood stratum: predominant: Quercus robur, Populus nigra, Rubus fruticosus, Prunus spinosa, Salix species; scattered: Betula verrucosa. The tree stratum is lacking.

Biotope F (Figure 6)

Steep slope near a pond in the woods.

1. Subsoil: variegated sandstone with a slight weathered layer, not exposed.

2. Surface stratum: in about equal proportions raw humus, a mat of grassroots and stalks, and moss.

3. Herb stratum: predominantly grasses, Melampyrum, Hedera helix; scattered: Plantago media, lanceolata, Fragaria vesca, Aspidium filix mas, Daucus

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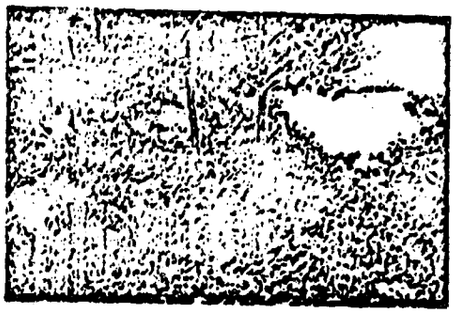

Figure 7.

carota, melilot, Achillea millefolia, Helleborus foedidus, Teucrium scorodonia, Saponaria off., Urtica dioeca, Viola spec., Hieracium boreale, Filipendula ulmaria.

4. Brushwood stratum: predominant: Quercus robur, Corylus avellana, Acer pseudoplatanus, Viburnum lantana, Rubus fruticosus; scattered: Carpinus betula, Cornus sanguineus, Evonymus europaeus, Betula verrucosa, Rosa canina, Populus nigra, Ligustrum vulgare, Prunus avium, Rubus idaeus, Crataegus monogyna, Frangula alnus, Viburnum opulus, Salix alba. Tree stratum lacking.

Biotope G (Figure 7)

Continuation of biotope F about 70-100 m below it, immediately adjacent to the bank of the pond, but entirely separated from biotope F.

1. Subsoil: very humous, partly marshy, loamy soil.

2. Surface layer: mosses or in places a thick layer of raw humus; grass-root mat more toward the slope.

3. Herb stratum: gramineae, juncaceae, Rumex acetosa.

4. Brushwood stratum: Rubus fruticosus, Corylus avellana.

5. Tree stratum: predominating: Alnus, Populus nigra; in addition, Carpinus betulus, Fagus silvatica, Quercus robur, Betula verrucosa, Salix species.

This description of seven isolated habitats shows that the tree stratum may be lacking when a well-developed brushwood stratum is present that affords adequate protection against strong sunshine and drying out. The photographs were all taken between 12:00 noon and 1:00 p.m., when the sun was at its highest, and in clear, sunny weather, in order to demonstrate the distribution of light and shade and the extent to which the effect of sunshine is excluded. The photographs also show that the areas are more or less readily accessible (through paths, broad game trails, small clearings, and the like). This circumstance seems to me to be characteristic of all firefly habitats, since all the specimens I was able to find, of whatever stage of development, were in open areas or in the edges of denser growth, not more than two or three meters into the thicket at most. This is attributable to the fact that the snails that serve as food for the larvae of both species (Chapter C III 2) are dependent on the marginal and the more open areas, which because of conditions of light are covered with a heavier herb stratum, and also that the imagines -- both the male for flying and the female as a site for showing an attractive light — prefer open terrain (cf. appetency).

Of the twelve biotopes that were constantly under ob-

servation, seven of which were chosen for description here, nine were inhabited jointly by Lampyris and Phausis. This finding is all the more surprising in view of the fact that in the literature with which I am acquainted no observation is to be found concerning the simultaneous occurrence of the two species in the same biotope. But the fact is also remarkable for the reason that where the imagines of the two species appear at the same time (Chapter C II 2) there could be complications in finding the sexes, since the sexually mature animals (except for Lampyris males), the larvae, and the pupae of both species luminesce. This question did in fact play a big part in my later experiments concerning the sexual behavior. Biotopes C and G are among the three places where only Phausis splendidula occurs. The close connection with open water or ground water is suggested not only topographically, but also by the stock of decidedly hydrophilous plants (sphagnum, rushes, horsetail, ferns, cyperaceae, salix, alder), which in the other biotopes are less conspicuous or entirely lacking or are represented by plants less adapted to the water. These relationships are clearly shown by the neighboring biotopes C and D and by F and G.

A little watercourse connects biotopes C and D, but on the way from the source area (biotope C) to biotope D with a high groundwater level (depression in the terrain) flows through a typical sandy Cicindela habitat (at about 800 m) that effects a sharp separation of the two biotopes. The head of the valley (biotope C) opens to the north and is surrounded on all sides by high spruces and birches which shade the biotope proper even when the sun is high. (The dew remains on hot days until the afternoon hours.) Biotope D on the other hand is exposed to diffuse sunlight at various hours of the day; plants appear that demand less moisture but more light, such as melilot, plantago, dandelion, stinging nettle, melampyrum; the brushwood is more open and the ground less damp. The same striking peculiarities are shown by the higher, drier biotope F (north slope of the hill) in comparison with the damp biotope G which is exposed to the pond on the north. Coniferous forest always forms a strict boundary, as is shown by C, F, and G. The separation between F and G and between two other biotopes innabited by both species 30 m above F is formed in each case by a dense mixed crop of spruce and pine of 70-100 m and 30 m in width respectively. This forms such a definite boundary that of some 150 Phausis larvae and 30 Phausis females caught there I did not find even a single specimen within the sharply defined area covered by unbroken pinestraw. (The more mobile males occasionally do fly into the coniferous plantation.)

The area of the biotopes varies greatly, in those with which I am acquainted from a few square meters (biotope D about 60 square meters) to several thousand.

2. Habitat

I found most of the many hundred larvae of the two species in the ground stratum, which is their real habitat, to a greater extent for Phausis than for Lampyris, the larvae of which are occasionally found in the herb stratum up to a meter from the ground in search of prey. This is not particularly surprising, since it is precisely here that the best cover is to be found, where it can be shown that even on hot days the relative humidity does not drop below 80% at any time of day, where no direct sunlight reaches, where the extremes of the microclima are largely leveled out, and where — last but not least — the prey is to be found. Moreover the annual defoliation provides a cover for protection and wintering that offers good insulation and is readily accessible to the ground insects, which are relatively slow and not adapted to burrowing. That they are so much bound to the ground stratum is the more striking in view of the fact that they are well equipped to climb with sharp claws and pygopodium (they can even climb up unpolished glass surfaces if these are a little inclined from the vertical).

In order to determine the place of abode during the day in the open, soil samples up to 20 cm in depth were systematically studied by digging out and spreading the crumbled material on a white cloth, and it was found that the larvae of both species in open terrain stayed exclusively in more or less loose soil material (humus, raw humus, grass mat, moss), retiring not at all or only occasionally during the day into the actual topsoil itself. (Cf. wintering, Chapter C III 1a.) Because of its slowness and tediousness this method is unsuitable for determining the density of the population even when the population is relatively dense, since too great areas would have to be studied with painstaking exactness for that. In general it may be said that the density of population decreases with increasing size of the biotope. For a study of the density of population see the findings on rate of multiplication and the like under Chapter C II 3. The next chapter gives further information concerning the relation to the ground stratum.

3. Ecological Factors

My plan was first to study the optimal or preferred conditions of the natural environment. The result could then be taken into account in laboratory experimentation,

so as to ensure as natural as possible behavior of the animals. In addition study of the ecological factors would help to make possible successful growing of my animals without too great losses, and since this chapter supplements other biological observations, it was left in the biological and ecological section.

For the investigation of decisive factors experiments on the choice of "micro-" habitats were carried out, the preferences determined in moisture, brightness, and temperature gradients, and laboratory and outdoor observations resorted to on phototaxis and scototaxis.

The following observations are to be considered as preliminary experiments on the complex problem of ecological factors.

Experiments on Choice of Habitat

Phausis larvae were kept temporarily in a petri dish (diameter 15 cm). About half the dish was covered with moist red sand (soil from various natural biotopes) and the other half with raw humus. It was found that the larvae sought the surface of the humus half, not only at night but also by day (at about 400 lx of diffuse daylight); this thus rules out interpretation of their behavior as a scototactic reaction (relatively lighter sand as against darker humus). This observation led me to further experiments: Larvae of the two species (30 Lampyris, 40 Phausis) were put into a petri dish (20 cm in diameter and 10 cm high) in artificial microhabitats in a normal day-and-night cycle (night from 6:00 p.m. to 8:00 a.m.; day = max. 500 lx), with the bottom of the petri dishes covered as follows (always with about 100% relative humidity and an average of 15-17° C):

1. One half sand (variegated sandstone sand), one half leaf litter over sand (Table 1, Figure 8).

2. One half sand (variegated sandstone sand), one half raw humus over sand (Table 2, Figure 9).

3. One half sand, one half cultivated soil (loamy soil of limestone content) (Table 3, Figure 10).

4. One half cultivated soil, one half leaf litter over cultivated soil (used only for Phausis, Table 4, Figure 11a).

5. One half cultivated soil, one half raw humus over cultivated soil (used only for Phausis, Table 5, Figure 11b).

6. One quarter sand, one quarter cultivated soil, one quarter leaf litter, one quarter raw humus (Table 6, Figures 12a and 12b).

7. One quarter sand, one quarter cultivated soil, one quarter leaf litter, one quarter pinestraw (Table 7, Figures 13a, 13b).

Table 1. 1/2 sand, 1/2 leaf litter.

Lampyris (30 individuals)			Phausis (40 individuals)		
Time	Sand	Leaves	Time	Sand	Leaves
14:00	placed on sand	-	14:00	placed at dividing line	
17:00	1	29	17:00	12	28
19:00	4	26	19:00	10	30
24:00	7	23	24:00	10	30
5:00	3	27	5:00	4	36
10:00	2	28	10:00	2	38
15:00	0	30	15:00	2	38
20:00	3	27	18:00	11	29
1:00			20:00	8	32
6:00			1:00	4	36
11:00			6:00	1	39
12:00	put back on sand	-	11:00	1	39
13:00	3	27	12:00	put back on sand	
16:00	2	28	17:00	39	1
19:00	3	27	22:00	10	30
23:00	1	29	3:00	4	36
4:00	3	27	8:00	2	38
9:00	2	28		after two days	
14:00	2	28	11:00	0	40
			14:00	0	40

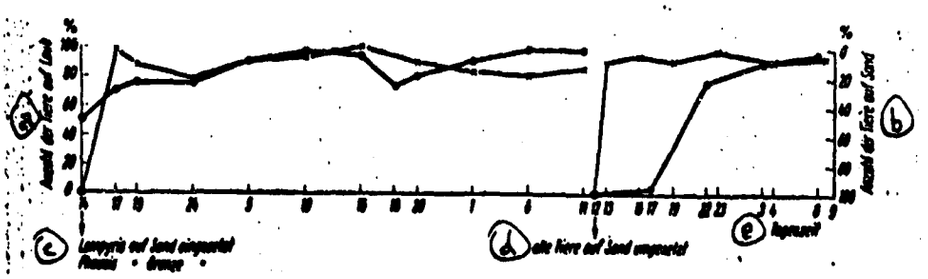

Figure 8. Choice between sand and leaf litter. Lampyris xxx, Phausis ooo; a beginning of experiment and resetting of the insects.
a) number of insects on leaves; b) number of insects on sand; c) Lampyris placed on sand, Phausis at the dividing line; d) all insects put back on sand; e) time of day.

These microhabitats were checked every five hours after it had been found that shorter intervals did not change the results. Exceptions were made in order to demonstrate specific effects in the behavior of the insects (cf. in the tables the time check in the evening and morning hours).

Table 2. 1/2 sand, 1/2 raw humus.

Lampyris (30 individuals)			Phausis (40 individuals)		
Time	Sand	Humus	Time	Sand	Humus
14:00	placed on sand		14:00	placed at dividing line	
15:00	24	6	18:00	8	32
17:00	23	7	23:00	12	28
19:00	27	3	4:00	16	24
24:00	22	8	9:00	17	23
5:00	18	12	14:00	12	28
10:00	23	7	19:00	11	29
10:00	moved to humus		24:00	3	37
15:00	17	13	5:00	4	36
17:00	17	13	10:00	2	38
20:00	18	12	13:00	1	39
1:00	23	7	13:00	put back on sand	
6:00	21	9	18:00	8	32
9:00	12	18	23:00	0	40
	after two days		4:00	4	36
11:00	19	11	9:00	2	38
14:00	15	15	14:00	2	38
			19:00	7	33
			24:00	4	36
			5:00	8	32
			10:00	7	33
				after two days	
			13:00	2	38

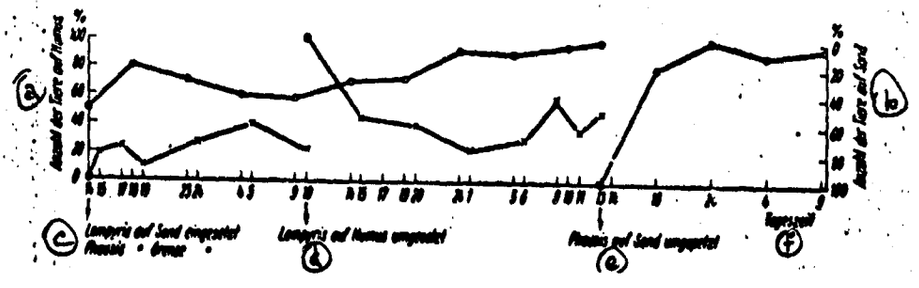

Figure 9. Choice between sand and raw humus. Symbols as in Figure 8. a) no. of insects on humus; b) no. of insects on sand; c) Lampyris placed on sand, Phausis at the dividing line; d) Lampyris put back on humus; e) Phausis put on sand; f) time of day.

The larvae of both species always seek out the environment with the greatest degree of cover. It is nevertheless striking that the Lampyris larvae have less preference for raw humus than sand, while the Phausis larvae, as expected,

Table 3. 1/2 sand, 1/2 cultivated soil.

Lampyris (30 individuals)			Phausis (40 individuals)		
Time	Sand	Cultivated Soil	Time	Sand	Cultiv. Soil
14:00	placed at dividing line		14:00	placed at dividing line	
18:00	20	10	17:00	motionless at the same	
23:00	23	7		place, some still on	
4:00	27	3		their backs	
9:00	28	2	18:00	20	20
14:00	26	4	19:00	20	20
19:00	26	4	24:00	8	32
24:00	23	7	5:00	1	39
2:00	19	11	10:00	1	39
5:00	20	10	15:00	2	38
10:00	27	3	19:00	11	29
14:00	25	5	20:00	5	35
14:00	placed on cultiv. soil		1:00	0	40
19:00	21	9	6:00	1	39
24:00	23	7	11:00	1	39
5:00	27	3	15:00	1	39
10:00	26	4			
15:00	24	6			

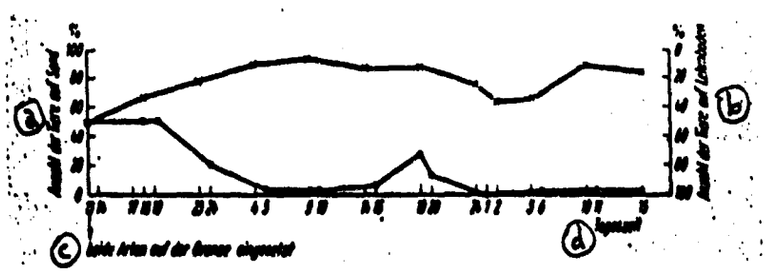

Figure 10. Choice between sand and loamy soil. Symbols as in Figure 8. a) number of insects on sand; b) number of insects on loamy soil; c) both species placed at the dividing line; d) time of day.

give the preference quite decidedly to the raw humus. An equally different behavior of the two larvae is shown in the choice between sandy soil and loamy soil of limestone content (in the table = cultivated soil), Phausis preferring the loamy soil, Lampyris the sand. That Phausis also prefers leaves or humus to loamy soil is shown by Table 4-5 and Fig. 11. In the experiments with four choices the clear preference for leaf litter is evident in all cases. The number of insects in the other parts is usually considerably below 20% except during the evening and night hours. This difference

Table 4-5. 1/2 cultivated soil, 1/2 leaf litter (left column) or raw humus litter (right column). Phausis (40) in each case.

Time	Cultivated Soil	Leaves	Time	Cultivated Soil	Humus
14:00	placed at dividing line		14:00	placed at dividing line	
17:00	4	36	18:00	1	39
19:00	6	34	23:00	8	32
24:00	5	35	4:00	15	25
5:00	1	39	9:00	15	25
10:00	1	39	14:00	14	26
15:00	1	39	19:00	9	31
18:00	12	28	24:00	0	40
20:00	7	33	5:00	3	37
1:00	0	40	10:00	2	38
6:00	0	40	13:00	2	38
11:00	0	40	13:00	moved to cultiv. soil	
12:00	moved to cultivated soil		18:00	7	33
17:00	38	2	23:00	3	37
22:00	14	26	4:00	6	34
3:00	6	34	9:00	4	36
8:00	3	37	14:00	4	36
	after two days		19:00	16	24
11:00	3	37	24:00	11	29
14:00	3	37	5:00	8	32
			10:00	7	33
				after two days	
			13:00	1	39

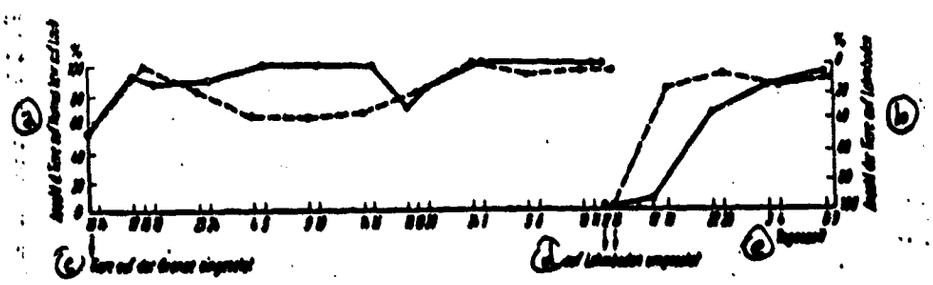

Figure 11a,b. Choice between humus and loamy soil (broken line) and between leaf litter and loamy soil (solid line). a) number of insects on humus and leaves respectively; b) number of insects on loamy soil; c) animals placed along the dividing line; d) moved to loamy soil; e) time of day.

between day and night is also clearly shown in the course of the "leaf litter curve." The leaf litter thus evidently serves as the sole refuge during the day. Only at night is this area deserted for the search for prey (not only in ex-

Table 6. 1/4 each: sand, cultivated soil, leaf litter, raw humus.

Lampyris (30 individuals)					Phausis (40 individuals)				
Time	Sand	Cultivated Soil	Leaf Litter	Raw Humus	Time	Sand	Cultivated Soil	Leaf Litter	Raw Humus
15:00	put in at the boundary point				15:00	put in at the boundary point			
17:00	3	2	25	—	20:00	9	3	16	12
23:00	15	—	14	1	1:00	2	10	24	4
8:00	16	2	11	1	6:00	3	7	15	15
9:00	2	—	27	1	11:00	—	6	29	5
14:00	1	—	28	1	17:00	—	5	32	3
19:00	1	—	29	—	21:00	2	5	29	5
24:00	1	1	28	—	2:00	2	7	22	9
5:00	1	2	25	2	7:00	1	5	29	5
10:00	2	1	25	2	12:00	1	3	29	7
	after four weeks				12:00	replaced as at the beginning			
10:00	1	1	24	1	17:00	4	1	4	4
15:00	—	1	29	—		(27 larvae still at center)			
19:00	2	1	26	1	22:00	2	3	18	17
23:00	—	3	22	5	3:00	—	16	13	11
9:00	2	—	27	1	8:00	—	7	21	12
9:00	replaced as at the beginning (only 25 larvae)				13:00	—	7	21	12
					18:00	—	7	21	12
10:00	3	—	15	7	23:00	1	18	18	3
15:00	—	—	23	2	4:00	—	7	23	10
20:00	1	3	20	1	9:00	—	7	23	10
1:00	1	1	19	4	14:00	—	7	23	10
6:00	2	2	20	1	19:00	1	10	21	8
11:00	2	—	21	2	24:00	3	3	24	10
16:00	—	2	21	2	8:00	—	1	36	3
21:00	—	1	22	2		after two days			
2:00	2	1	22	—					
7:00	2	1	22	—	11:00	—	4	35	1
12:00	2	—	22	1					
12:00	replaced as at the beginning								
13:00	1	—	24	—					
17:00	—	—	25	—					
22:00	1	3	19	2					
3:00	4	3	16	2					
8:00	3	2	19	1					
13:00	—	—	24	1					

periments but also in suitable cases in nature, e.g. when a road runs through a biotope and the like). Questions of the rhythm of activity are dealt with in a chapter to themselves. Let us merely mention at this point how very much the Phausis larvae differ from the Lampyris larvae with respect to their

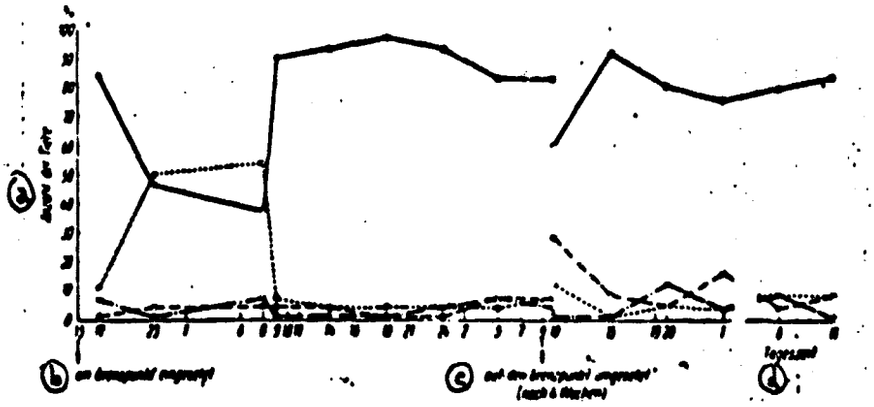

Figure 12a. Choice of Lampyris larvae (for sand ·····, for loamy soil -·-·-, for leaf litter ——, for raw humus ——). a) number of larvae; b) set at the focal point; c) set back at the focal point (after 4 weeks); d) time of day.

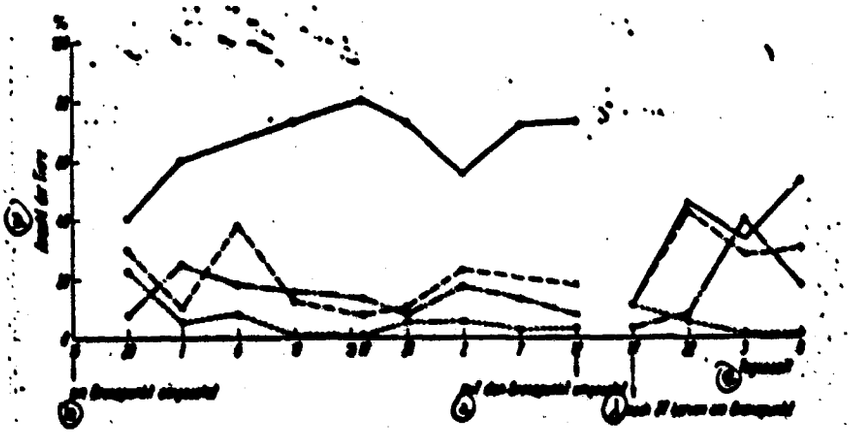

Figure 12b. Choice of Phausis larvae. Notation same as for Figure 12a. a) number of larvae; b) set at the focal point; c) set back at the focal point; d) 27 larvae still at focal point; e) time of day.

activity (Phausis in the daytime especially!). -- The preference for leaf litter can be seen in nature from the mere fact that the larvae of both species live exclusively under leaf-bearing bushes and trees. It should be mentioned here that for each experimental arrangement the insects were checked several times for several days at a time. Tables 1-7 are intended to demonstrate that and the graphs (Figures 8-13) to make it possible to compare the results for the two species better, the number of individuals being reduced there to percentages.

Table 7. 1/4 each: sand, cultivated soil, leaf litter, pinestraw.

Lampyris (25 individuals)					*Phausis* (40 individuals)				
Time	Sand	Cultivated Soil	Leaf Litter	Pinestraw	Time	Sand	Cultivated Soil	Leaf Litter	Pinestraw
20:00	put in at the boundary point				20:00	put in at the boundary point			
22:00	2	2	17	4	22:00	5	9	19	7
1:00	1	4	17	3	1:00	3	9	22	6
6:00	1	2	19	3	6:00	3	3	31	3
11:00	1	2	20	2	11:00	2	2	34	2
16:00	—	2	22	1	16:00	1	1	35	3
19:00	2	1	19	3	19:00	3	7	21	9
23:00	2	2	18	3	23:00	—	7	22	11
4:00	—	2	20	3	4:00	1	3	31	5
9:00	—	—	21	4	9:00	—	3	33	4
14:00	—	1	23	1	14:00	—	3	33	4
14:00	replaced as at the beginning				14:00	replaced as at the beginning			
15:30	—	3	21	1	15:30	all still at the center, some still on their backs			
					18:00	all still at the center, in normal posture			
19:00	4	2	15	4	19:00	11	11	11	7
24:00	—	3	22	—	24:00	—	13	17	10
5:00	1	1	20	3	5:00	1	—	35	4
10:00	1	2	22	—	10:00	—	—	37	3
15:00	2	—	23	—	15:00	—	—	37	3
20:00	—	2	20	3	20:00	9	8	16	7
1:00	1	1	21	2	1:00	—	2	33	5
6:00	—	3	21	1	6:00	1	2	34	3
10:00	2	2	20	1	10:00	2	—	37	1
	after eight days					after eight days			
14:00	—	—	25	—	14:00	—	4	29	7

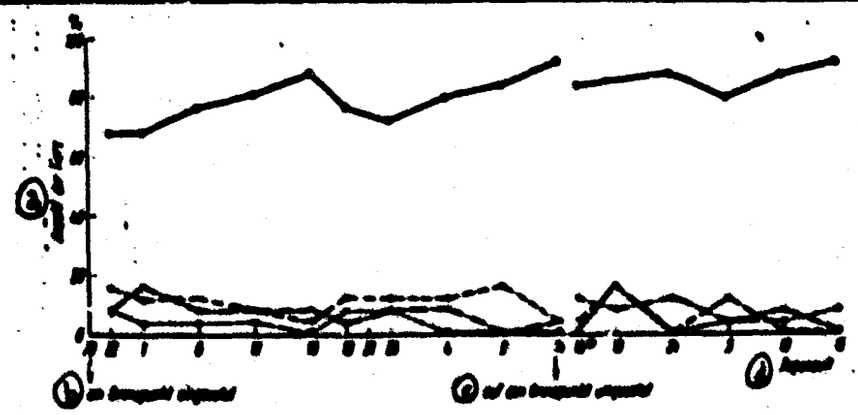

Fig. 13a. Choice of the *Lampyris* larvae (for sand ·····, loamy soil -·-·-, leaf litter ———, pinestraw ———). a) no. of larvae; b) set at focal point; c) reset at focal point; d) time of day.

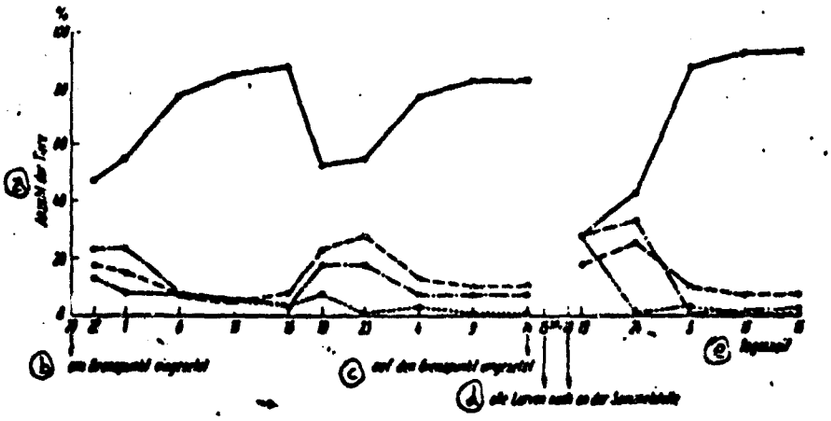

Figure 13b. Choice of the Phausis larvae. Notation as for Figure 13a. a) number of larvae; b) placed at the focal point; c) set back at the focal point; d) all larvae still at the focal point; e) time of day.

Behavior in the Humidity Gradient, Hydrokinesis, Loss of Water in the Drying Chamber

To determine the preference in the humidity gradient, a humidity gradient of nearly 100-0% was produced in the usual way by means of salt solutions: H_2O 100%, K_2SO_4 96-100%, NaCl 72-76.5%, $CaCl_2$ 35%, $ZnCl_2$ 10-20%, P_2O_5 (dry) 0% relative humidity. Immediately above the vessels was a runway of netting; the whole apparatus was hermetically sealed (Figure 14).

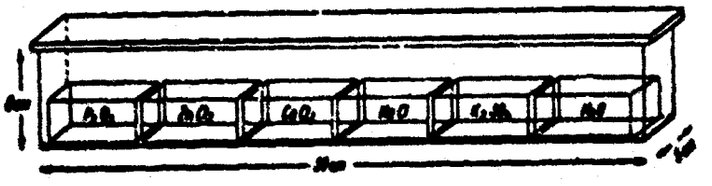

Figure 14. Humidity gradient. Explanation in the text.

Results for Lampyris larvae (Table 8)

Temperature: 20° C
Lighting: complete darkness
Number of larvae: 15 (of various ages and varying physiological state)
Observation: hourly
The larvae were put into the apparatus over the P_2O_5.

Table 8. Number of larvae [Lampyris] and distribution over:

Hours from Beginning of the Experiment	P_2O_5	$ZnCl_2$	$CaCl_2$	NaCl	K_2SO_4	H_2O
1.	6	-	2	1	-	6
2.	3	-	2	1	4	5
3.	2	1	2	2	1	7
4.	2	2	1	2	1	7
5.	2	1	1	2	1	8
6.	3	1	-	3	1	7
7.	1	1	1	2	4	6
8.	1	-	1	-	5	8
9.	1	1	-	4	3	6
10.	-	-	-	2	4	9
11.	-	1	-	1	2	11
12.	-	-	-	2	3	10
13.	-	-	-	2	4	9
14.	-	-	1	2	3	9
15.	-	-	1	2	2	10
16.	-	-	1	1	3	10
17.	-	-	1	3	3	8
18.	set back over the P_2O_5					
19.	3	10	1	-	-	1
20.	3	9	2	-	-	1
21.	4	6	2	2	-	1
22.	4	4	1	4	1	1
23.	3	2	1	2	4	3
24.	-	3	1	3	5	3
25.	-	2	2	5	3	3
26.	1	1	3	3	3	4
27.	-	1	1	4	6	3
28.	-	1	1	2	6	5
29.	-	-	1	2	5	7
30.	-	-	1	2	6	6

Results for Phausis Larvae (Table 9)

All experimental conditions same as for Lampyris.

Table 9.

Hours from Beginning of the Experiment	P_2O_5	$ZnCl_2$	$CaCl_2$	NaCl	K_2SO_4	H_2O
1.	2	-	-	-	3	10
2.	-	-	-	1	10	4
3.	-	-	-	-	12	3
4.	-	-	-	-	12	3
5.	-	-	-	-	12	3
6.	-	-	-	-	12	3
7.	-	-	-	-	12	3
8.	-	-	-	-	12	3
9.	-	-	-	-	12	3
10.	-	-	-	-	12	3
11.	-	-	-	-	12	3
12.	-	-	-	-	12	3
13.	set back over the P_2O_5					
14.	1	5	7	1	1	-
15.	-	-	5	6	4	-
16.	-	-	3	6	5	1
17.	-	1	2	6	5	1
18.	-	-	1	6	7	1
19.	-	-	2	5	7	1
20.	-	-	2	4	8	1
21.	-	-	2	4	8	1
22.	-	-	2	4	8	1
23.	-	-	2	4	8	1

The two tables and Figures 15a and 15b show a very definite irreversible preference for relative humidities between 80 and 100%. The Phausis larvae, otherwise more sluggish (cf. akinesis and locomotion, Chapter E I), react considerably more quickly and sharply here than the Lampyris

larvae. While the Phausis larvae, whose natural biotope is more humid, do not prefer the most humid-chamber, they give all the more decided preference to the K_2SO_4 chamber with about 96-100%.

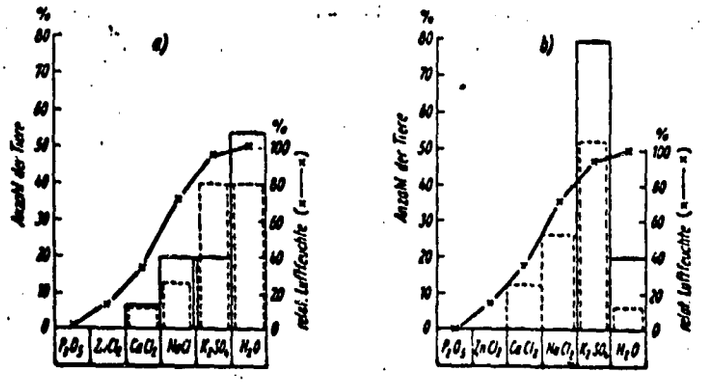

Figure 15. Behavior in the humidity gradient: Lampyris (a), Phausis (b). ——— Results 17 hours after beginning of the experiment; ···· results after the larvae were set back at 0% relative humidity (P_2O_5) after 12 hours. Scale at left: number of larvae; scale at right (of each graph): relative humidity.

If water is dripped into a dried-out cultivation dish, the larvae are quickly oriented and run to the moist spot. The hydrokinesis is shown by the following experiments: The larvae (Lampyris) were kept for a few days beforehand at about 70-80% relative humidity and without an opportunity to take in water and then put into a petri dish 2 cm deep and 15 cm in diameter; this was covered with a dark handkerchief and lighted with a weak, diffuse overhead light (about 30 lx). The bottom was covered with sand dry as dust. At one end of the dish a little water was dripped in until half the dish was moistened, with a slight discoloration of the sand (red sand). At the place where the water was dripped in a drop of water was placed on the glass wall 1/2 cm from the bottom for drinking (see pages 60 ff.), as the point of highest water concentration so to speak. All five larvae not only reached the moist zone but stayed in it most of the time for hours. The first one reached the moist zone after 5 minutes, the last after 12 minutes; the water drop was used by three larvae for drinking (the animals were naturally not all in the same physiological state). When they occasionally got into the dry zone they often turned around immediately and not infrequently went back to the drop of water to drink. The attempt to climb up the glass wall was made only in the dry part.

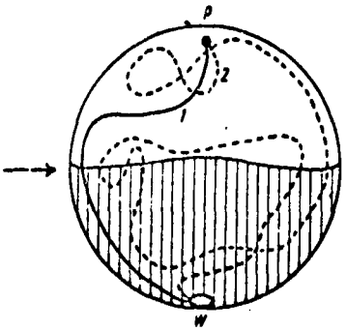

Fig. 16. P = starting point for both larvae; W = drop of water; → attempt to climb up the glass wall.

Figure 16 shows the paths traced by two of the larvae.

In cultivation dishes that are drying out there is a fast drop in body volume, both in the longitudinal and in the dorsiventral axis. In order to demonstrate the effect of the drying environment more precisely, larvae of Lampyris and Phausis were put into an atmosphere of 45-48% relative atmospheric humidity at 17-18° C and their water loss determined hourly by decline in weight on the analytical scales. For comparison a freshly killed larva was weighed in each case.

The results are shown in Figures 17a and 17b. The body weight de-

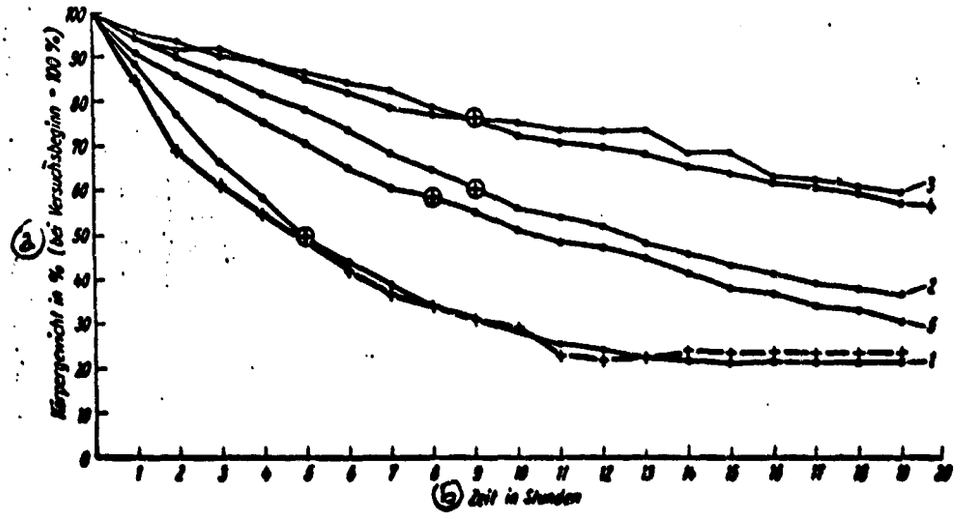

Figure 17a. Decrease in body weight at 45-48% relative atmospheric humidity and 17-18° C (Lampyris). 1-5 individual larvae, + + + comparison figures for a killed larva, ● death of the subject. a) body weight in % (weight at beginning of experiment = 100%); b) time in hours.

creases continuously down to a certain percentage; the curve then runs asymptotically to the abscissa down to the constant weight of the air-dried body. Death occurs in Phausis between the sixth and seventh hours after the beginning of the experiment, in Lampyris very irregularly

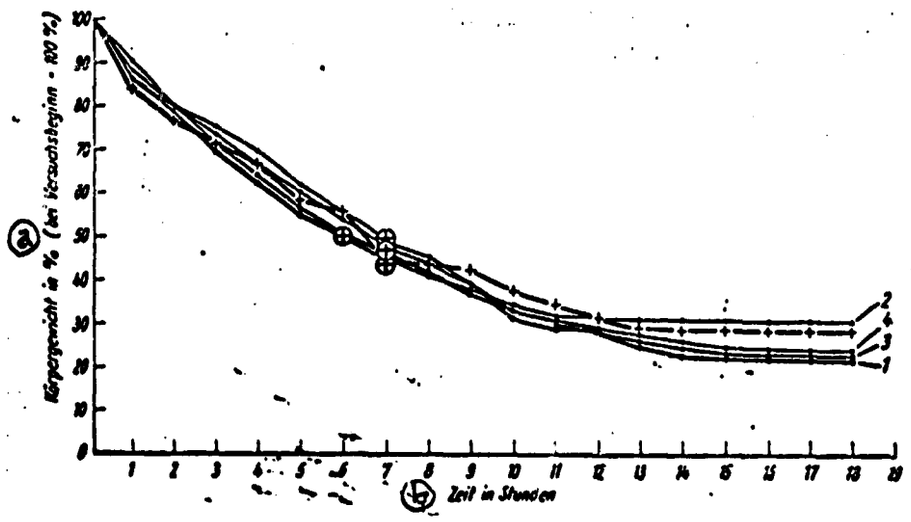

Figure 17b. Decrease in body weight at 45-48% relative atmospheric humidity and 17-18° C (Phausis). 1-3 individual larvae, 4 averages for five larvae; other signs as in Figure 17a. a) body weight in % (weight at beginning of experiment = 100%); b) time in hours.

or not at all (cf. curve 3, Figure 17a, and drinking, pages 60 ff). If we compare the curves for the experimental subjects with those of the killed test animals, we find that in Phausis all the curves follow very closely the curve of the killed animals, and in fact almost coincide with it; in the case of Lampyris that is true only of curve 1, while curves 2-5 run much flatter. This circumstance suggests that Phausis larvae lack any regulatory mechanism against drying out, but that Lampyris larvae can protect themselves moderately against drying out. That is also the only way to explain the fact that one larva was able to survive. This curve 3 shows repeated sudden drops with temporary constancy of body weight. The course of curve 1, Figure 17a (Lampyris), which nearly coincides with that of the killed animal, may perhaps be attributed to the larva's having been seriously injured for some reason. That would also explain the relatively early death (after the fifth hour).

In the course of this investigation characteristic variations in behavior occurred which were repeated in all the individual larvae. Both species appeared surprisingly active within the first hour; akinesis, which can last for hours in Phausis larvae, was reduced to a few seconds and later did not occur at all. After about four hours neither species of larva showed any more coordinated locomotive movements (except for the one that survived, whose movements only

became somewhat uncoordinated after 19 hours). Just an hour later nearly all the larvae of both species ceased all locomotion (with the exception already mentioned); they moved only in response to powerful mechanical stimuli; the reaction of turning over was lacking; death followed soon after.

These findings too indicate that both species react very sensitively to extreme conditions, and that like many pronounced ground animals they are almost or completely without protective adaptations against drying out (by direct sunshine, insufficient ground cover, high temperature, etc.). The possibility of a slight adaptation of Lampyris also suggests the ability to inhabit areas where Phausis is lacking (see pages 29 and 31).

Phototaxis, Behavior in the Brightness Gradient, Scototaxis

That the factor of light has great ecological significance is indicated by my intensive but fruitless searches in the daytime in well-populated habitats, and also the reaction to artificial light occasionally observed. Thus for example the larvae in the evening or at night in the vessels in which they were kept (without leaf litter and the like) stayed on the side of the vessel away from the light, and when the direction of the light changed they always turned negatively phototactically. With diffuse overhead light (500-700 lx) the larvae crawl toward a 5 x 5 cm black wall set up at a distance of 20 cm and follow even slight horizontal shifts of this wall.

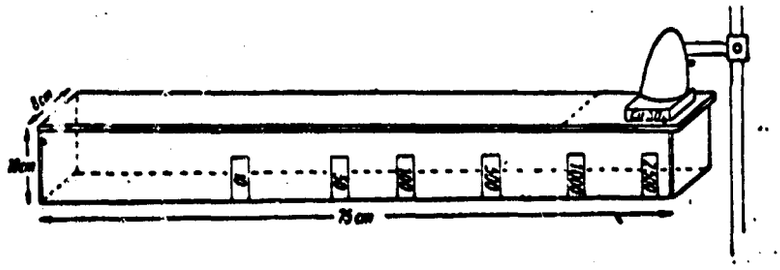

Figure 18. Light gradient. The sleeve used to darken it is not shown. The figures on the apparatus indicate the brightness in lux. Other explanations and dimensions are given in the text.

For closer study of the phototactic behavior I used a light gradient (Figure 18). It consisted of a closed glass case 75 cm long, 8 cm wide, and 10 cm high and a removable glass cover plate. This apparatus was covered with a sliding mantle of black paper except for one end that remained open. That end was lighted vertically from above with a small vertically sliding electric lamp with a shallow tray of $CuSO_4$ between the lamp and the case to absorb the heat. The bottom was covered to a depth of 1 cm with uniformly moist sand. The apparatus was calibrated in the dark from below with the bottom shade removed (before the sand was put in) with a light meter (Gossen's "Trilux," measuring unit "candela lux" = "neulux") until, by shifting the

black paper mantle and the lamp a usable brightness gradient had been produced, with the following graduation: 2500-1000 lx = 11 cm of the length, 1000-500 = 8 cm, 500-100 = 10 cm, 100-50 = 8 cm, 50-10 = 11 cm, 10-0 (0 lx = no longer measurable with the instrument) = 27 cm of the length.

Experimental conditions for both species:
Temperature: 20° C
Relative humidity in the apparatus: 80-100%
Number of larvae: 30
Start of experiment: 1:00 p.m.
Observation: hourly (except during the night hours).

The larvae, which had been habituated to diffuse daylight (500-700 lx) for six hours in the ordinary diurnal rhythm, were placed in the 500-1000 lx section.

Table 10. *Lampyris noctiluca* (Figure 19a)

Time	0 Lux	10 Lux	50 Lux	100 Lux	500 Lux	1000 Lux	2000—2500 Lux
14.00	7	5	4	4	3	6	1
15.00	11	3	3	4	4	5	—
16.00	10	6	3	2	2	6	1
17.00	17	4	3	2	1	3	—
18.00	11	5	5	3	2	4	—
19.00	17	4	1	2	4	1	1
20.00	18	7	2	1	2	—	—
	replaced in 500—1000 Lux (20.00)						
21.00	17	6	3	1	2	1	—
22.00	16	6	2	3	1	2	—
1.00	22	4	2	—	—	—	—
	replaced in 500—1000 Lux (1.00)						
2.00	17	7	3	—	2	1	—
5.00	24	5	1	—	—	—	—
	replaced in 500—1000 Lux (5.00)						
7.00	16	9	2	1	1	1	—
9.00	17	8	2	3	—	1	—
10.00	17	8	1	1	2	1	—
11.00	17	8	2	2	1	—	—

If we wish to compare the results for Lampyris and Phausis in the light gradient, we must — let us emphasize this once more — as in all our experiments that are based on speed of running and of general activity, take into account the fact that Phausis larvae are far more sluggish and are extremely sensitive to mechanical influences as compared to the agile, more insensitive Lampyris larvae.

The tables show that the larvae definitely react negatively phototactically, both in the daytime and at night. It is striking that after they are moved back at night the reaction occurs more rapidly (sometimes quite pronouncedly so) than in the daytime. Since the experiments were carried out independent of the normal day-and-night periodicity of brightness, we must assume a correspondingly different type of day-night activity rhythm, which

Table 11. *Phausis splendidula* (Figure 19b)

Time	0 Lux	10 Lux	50 Lux	100 Lux	500 Lux	1000 Lux	2000—2500 Lux
14.00	—	1	3	4	16	6	—
15.00	2	6	3	5	9	5	—
16.00	11	6	4	3	4	2	—
17.00	14	5	4	5	2	—	—
18.00	14	5	5	5	1	—	—
19.00	13	6	5	5	1	—	—
20.00	14	6	4	5	1	—	—
	replaced in 500—1000 Lux (20.00)						
21.00	4	6	6	7	6	1	—
22.00	8	3	8	6	4	1	—
1.00	14	5	4	7	—	—	—
	replaced in 500—1000 Lux (1.00)						
2.00	6	11	6	4	3	—	—
5.00	21	8	1	—	—	—	—
	replaced in 500—1000 Lux (5.00)						
7.00	10	5	10	3	2	—	—
9.00	14	6	6	3	1	—	—
10.00	14	6	6	4	—	—	—
11.00	14	6	6	4	—	—	—

seems to be endogenous to a certain extent. We might also interpret this behavior by saying that with the night hours a higher sensitization to light occurs, or that before (during the day) there existed a higher willingness to endure greater brightness. Once the state of insensibility is reached in the gradient there is hardly any further change with the beginning of day; the larvae remain motionless where they are, especially the Phausis larvae, but also the Lampyris larvae, which are otherwise so agile.

When the data were recorded at 14:00 (or one hour after the start of the experiment) the Phausis larvae were without exception oriented with the anterior end precisely toward the dark, the head completely hidden under the prothorax, which no doubt protects against light as well as other things; on subsequent checks no opposite orientation (and consequently direction of running) was ever observed. The Lampyris larvae occasionally went back to the brighter parts, but while there (especially in the 1000-2500 lx range) they moved remarkably fast and unsteadily, in a way comparable to a flight reaction. But in contrast to the imagines, no positive phototaxis could ever be observed in the larvae in any situation.

Toward red light the larvae of both species behaved totally indifferently, so that they could always be checked and observed under weak red light.

The running diagrams of Figures 20a and 20b are intended to illustrate the scototactic reactions under the following experimental arrangement (for larvae of both species):

A petri dish 25 cm in diameter and 12 cm high was surrounded to its full height with a white paper mantle; the uniformly moist sand in the bottom was covered with white filter paper, also moistened and divided into 8 equal sectors; and this arrangement was lighted from above with a uniform 800 lx.

Table 11. *Phausis splendidula* (Figure 19b)

Time	0 Lux	10 Lux	50 Lux	100 Lux	500 Lux	1000 Lux	2000—2500 Lux
14.00	—	1	3	4	16	6	—
15.00	2	6	3	5	9	5	—
16.00	11	6	4	3	4	2	—
17.00	14	5	4	5	2	—	—
18.00	14	5	5	5	1	—	—
19.00	13	6	5	5	1	—	—
20.00	14	6	4	5	1	—	—
	replaced in 500—1000 Lux (20.00)						
21.00	4	6	6	7	6	1	—
22.00	8	3	8	6	4	1	—
1.00	14	5	4	7	—	—	—
	replaced in 500—1000 Lux (1.00)						
2.00	6	11	6	4	3	—	—
5.00	21	8	1	—	—	—	—
	replaced in 500—1000 Lux (5.00)						
7.00	10	5	10	3	2	—	—
9.00	14	6	6	3	1	—	—
10.00	14	6	6	4	—	—	—
11.00	14	6	6	4	—	—	—

seems to be endogenous to a certain extent. We might also interpret this behavior by saying that with the night hours a higher sensitization to light occurs, or that before (during the day) there existed a higher willingness to endure greater brightness. Once the state of insensibility is reached in the gradient there is hardly any further change with the beginning of day; the larvae remain motionless where they are, especially the Phausis larvae, but also the Lampyris larvae, which are otherwise so agile.

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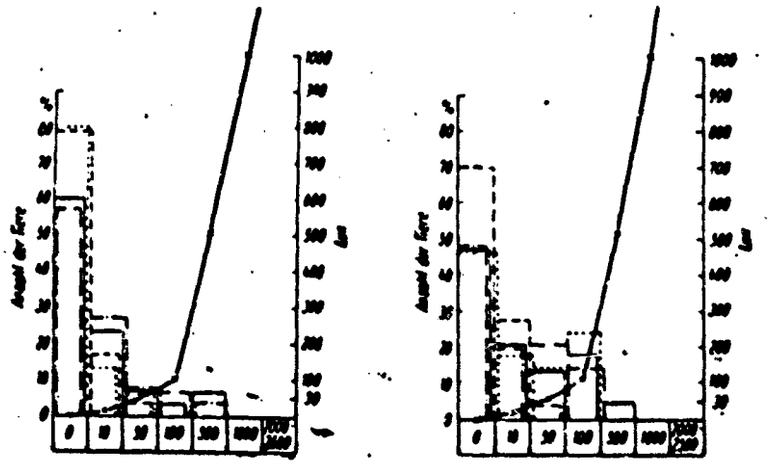

a b

Figure 19a. Behavior in the brightness gradient (Lampyris). ——— 7 hours after beginning of experiment; ····· 5 hours after replacing of the larvae; ——— 4 hours after replacing; -·-·- 6 hours after replacing. Scale at left of each graph: number of animals.
Figure 19b. Behavior in the brightness gradient (Phausis). Lines and scale same as for 19a.

The petri dish was covered with its regular lid to protect the larvae, which are extremely sensitive to draughts of air. The parts of the glass wall outlined in black in the figures represent a wall of black paper as high as the petri dish and reaching as far around it as indicated in the individual drawings. The circular segment of a sector amounts to about 10 cm. The experiments were carried out at night (cf. activity, Chapter C III 1 b).

For each experiment previously unused (unstimulated) larvae were used (10 Lampyris and 20 Phausis), put into the dish opposite the dark wall (at room temperature). The positions found (o) after a given time do not give a true picture, since the larvae when they reach the black wall make an attempt to climb up it or after a few unsuccessful attempts often move on, usually along the glass wall, since the light stimulus is still effective. The number of larvae had to be chosen in such a way that the experiment could be understood. If we compare the places where the larvae were particularly inclined to stay for a fairly long time (o) or attempted to climb up the wall (x), we find characteristic bunchings against the dark wall or at the change to the white wall; often the path traced comes to the limit of the dark wall and leads back to the dark wall. The paths, for the sake of clarity, are traced further in only a few characteristic cases after the dark wall has been reached. For each species only the paths of the five larvae are given that

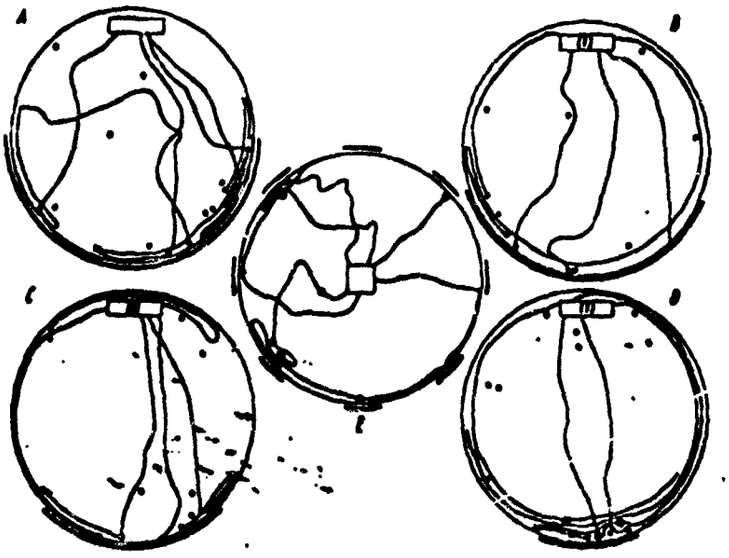

Figure 20a. Scototaxis in Lampyris larvae. ═══ starting point of all larvae opposite the dark wall ▬▬, ( ) = number of larvae that stayed at the starting point or returned to it. Other signs are explained in the text.

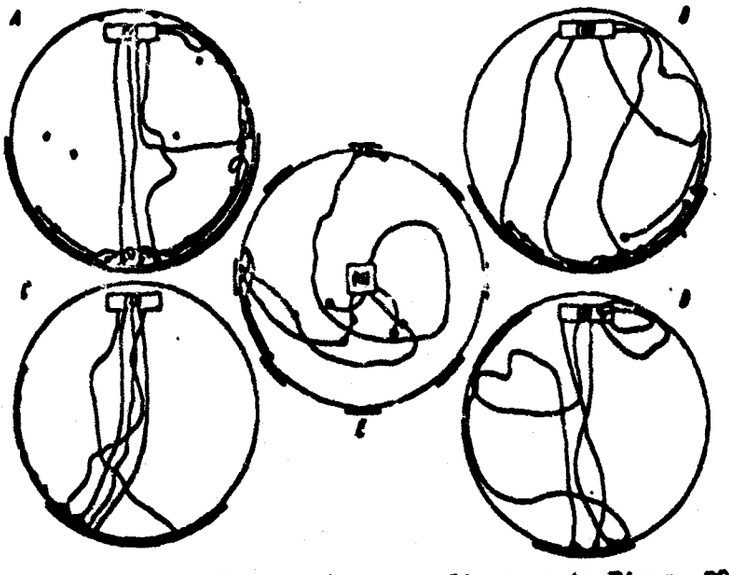

Figure 20b. Scototaxis in Phausis larvae. Signs as in Figure 20a and as explained in the text.

got in motion first. They show that the larvae of both species find the dark surfaces with some uncertainty in tracings D and E of Figures 20a and 20b, i.e. that from 25 cm away they are not able to move purposefully toward a dark wall

10 cm in width or from about 12 cm away toward one 2 cm in width. It should also be noted that the head is often hidden under the prothorax and that the animals at the point where they are introduced push themselves under parts of the bodies of their neighbors, so that sometimes bizarre tangles develop (especially in the case of Phausis); some paths traced show that the larvae occasionally return to the place where they were put in, since the animals that remain there represent a dark region, too. I was not able to carry out experiments with individual animals because in some larvae (especially Phausis larvae) akinesis often lasts for hours.

Preferendum in the Temperature Gradient

The temperature gradient (Figure 21) consisted of an iron bar 10 cm wide, 68 cm long, 1.5 cm thick with one end bent down. In one side of the bar were seven thermometers at intervals of 7 cm. On the bar was placed a glass case closed on all sides, 50 cm long, 8 cm wide, and 8 cm high. A freezing mixture and a small Bunsen burner provided in the usual way for the temperature gradient: 50°, 40.5°, 33.4°, 26.8°, 14.5°, 3 to 0°.

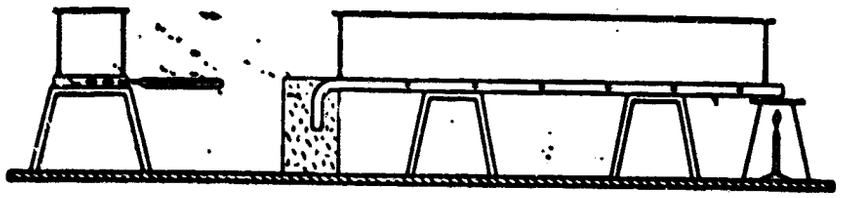

Figure 21. Temperature gradient. Explanation and dimensions in the text.

In this apparatus, at night and in darkness, with observation every half hour, 22 Lampyris and 17 Phausis larvae were tested.

Table 12. (L = Lampyris, P = Phausis)

Half-Hourly Checks	50° L	50° P	40.5° L	40.5° P	33.4° L	33.4° P	26.8° L	26.8° P	20.5° L	20.5° P	14.5° L	14.5° P	0—3° L	0—3° P
1.	—	—	—	—	—	—	4	4	8	5	4	7	6	1
2.	—	—	—	—	1	—	6	—	7	10	5	6	8	1
3.	—	—	—	—	—	—	4	—	12	1	6	N	—	5
4.	—	—	—	—	—	—	2	—	7	1	10	11	8	5
5.	—	—	—	—	—	—	3	—	6	12	8	5	5	—
6.	—	—	—	—	1	—	6	—	7	5	5	10	3	2
7.	—	—	—	—	—	—	6	—	4	5	5	10	7	2
8.	—	—	—	—	—	—	5	—	6	3	4	6	4	5
9.	—	—	—	—	1	—	9	—	5	1	3	9	4	7
10.	—	—	—	—	—	—	7	1	5	7	4	9	3	—
11.	—	—	—	—	—	—	6	1	9	7	6	7	1	2
12.	—	—	—	—	1	—	9	1	5	7	3	7	1	2
13.	—	—	—	—	—	—	9	1	7	7	5	7	1	2

Table 12 and Figure 22a,b show that the Lampyris larvae react less sensitively than the Phausis larvae and have a somewhat higher and broader

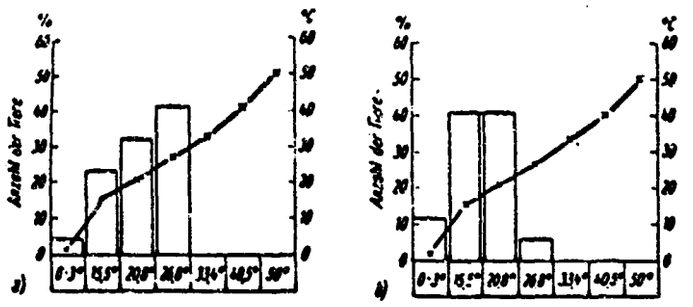

Figure 22a. Reactions of Lampyris larvae in the temperature gradient.
Figure 22b. Reactions of Phausis larvae in the temperature gradient. Scale at left of each graph: number of larvae in %.

temperature preferendum (cf. also geographic distribution, Chapter C I 4). That is in accord with the fact that Phausis occurs in biotopes that are better protected against light, moister, and cooler, while Lampyris larvae are much more often found in the marginal area of biotopes limited by humidity (e.g. in biotope B).

The absolute recoil temperature for Lampyris is between 40° and 33°. The larva rears the fore part of its body, lifts the first and second pairs of legs, at the same time making violent and hurried movements of the fore part of the body and of the head, which is quickly stretched forward and again drawn in; the motion of the antennae is also strikingly violent. The larvae never voluntarily went past the 40° C line.

The times spent by individual larvae (Lampyris) at various temperatures in the temperature gradient are shown below. The larvae were put in at 50°; the time taken from thermometer to thermometer (= 7 cm) after the akinesis brought on by the reaction to being moved and placed in the apparatus was:

Table 13.

Larva	50°	40,5°	33,4°	26,8°	20,8°	15,5°	8—0°
1.	15 sec	20 sec	20 sec	180 sec	•		
2.	15 sec	25 sec	80 sec	120 sec	200 sec	•	
3.	85 sec	10 sec	20 sec	30 sec	•		
4.	10 sec	30 sec	140 sec	250 sec	•		
5.	12 sec	28 sec	180 sec	50 sec	•		

• Stay of longer than 5 minutes.

This little series of experiments is intended to show how quickly after the akinesis has died out the larvae orient themselves on the relatively large surface (8 x 7 cm per field) and how the speed of running steadily decreases. No. 3 is interesting. After a longer period of orientation the larva flees all the faster from this constant stimulus into the tolerable temperature fields.

A similar behavior is exhibited by Phausis, but the flight reaction begins as early as the 30° zone, the larvae never went voluntarily beyond the 30° line, and the movements of the flight reaction look more violent and "desperate" than those of Lampyris; the larvae run uncoordinated and without direction, stumble, fall down, and often begin to luminesce after a stay of one minute at 50° C.

The test of speed of orientation came out as follows:

Table 14.

Larva	50°	40,6°	33,4°	26,8°	20,8°	15,5°	8—0°
1.	60 sec	25 sec	70 sec	180 sec	•		
2.	35 sec	55 sec	115 sec	240 sec	•		
3.	1)						
4.							
5.	start	35 sec	240 sec	•			
6.	at 40,6°	30 sec	30 sec	240 sec	•		

1) Began to glow after 10 sec, curled up, took firm hold with the pygopodium, remained lying motionless; when moved within one minute to normal temperature, they soon showed normal movement again.

A temperature of 50° C seems to have a more dangerous effect on the organism of the Phausis larvae than on Lampyris. Otherwise, in the progressive decline of reaction speed, the results show about the same conditions as with Lampyris, though Phausis may flee relatively faster than the very mobile Lampyris.

It is very surprising that the temperature intolerable to the larvae is as low as 30°, especially as such temperatures often occur outdoors; lower temperatures (around 0° C) are borne without noticeable reaction (e.g. rigor due to cold). This again shows clearly why the larvae avoid exposed localities.

4. Geographical Distribution

In the literature there are few statements about the geographical and horizontal distribution. E. Olivier [98] alone gives a sketchy description of the geographical areas of distribution of the four big groups of lampiridae (Lampyris, Luciola, Photinus, and Photuris). Vogel, who has published most extensively so far on the native lampyridae, also only cites Olivier. According to Olivier the Lampyrini (except Phausis, which also occurs in America) are inhabitants of the Palaearctic region, distributed throughout Europe and Asia, in the north as far as Finland and the Amur region, in the south to Borneo, Sumatra, and Java; in Africa only in a narrow Mediterranean strip, farther south in eastern Abyssinia, and from the equator to the Cape of Good Hope.

According to Borchert [11] Phausis splendidula is not to be found in

the European area north of the Hamburg-Köslin line, while in the west the boundary is approximately a line from Nancy to northern Italy and from there approximately to Tiflis [Tbilisi]. — Quite generally Lampyris noctiluca has a wider area of distribution. This species together with Photinus frigidus (American) extends farthest to the north, to southern Scandinavia (about 60° north latitude), England (not in northern Scotland and Ireland); it is found on the Iberian Peninsula, in the Apennine and Balkan Peninsula approximately to 42° north latitude; its area of distribution opens out on the east as far as northern China. The northern and southern distribution of the two species I can confirm from various excursions.

No information is available about the vertical distribution. That at least Lampyris occurs high in Alpine locations is shown by a find on the Hetzkogel, 1542 meters high, near Lunz in the Lower Austrian Alps, in the immediate vicinity of the peak. [see Note].

[Note] For the report of this find I am indebted to my friend N. Sischka, cand.rer.nat.

The geographical and perhaps also the vertical distribution show a greater tolerance with regard to temperature and exposure of the Lampyris species in contrast to Phausis, as indeed other biological investigations also indicate (Chapter C I 1-3). It is interesting in this connection to compare the average temperatures of the north, central, and south European areas, the main area of distribution of the two species in Europe. We have worked out the annual average, the combined average for the spring, summer, and fall months, and the averages for winter and summer months respectively (according to tables of the monthly temperature averages in Hann's Handbuch der Klimatologie (Manual of Climatology), Vol III, Klimatographie (Climatography), Stuttgart, 1911). From the south European area (not below 42° north latitude) the points Perpignan, Montpellier, Avignon, Marseille, Cannes, and Nice were chosen; from the central European, Frankfurt, Kaiserslautern, Nuremberg, Karlsruhe, and Stuttgart; from the north European (not above 60° north latitude, Mandal, Skudenes, Sandösund, Karlshamn, Göteborg, Jönköping, Visby, Stockholm, and Karlstad.

Table 15.

	Average for the Summer Months (May-August)	Average for the Spring, Summer, and Fall Months (April-October)	Average for the Winter Months (November-March)	Annual Average
South Europe	20.6° C	18.5° C	8.1° C	14.2° C
Central Europe	16.3° C	14.2° C	2.0° C	9.1° C
North Europe	13.7° C	11.3° C	0.1° C	6.6° C

The compilation shows that the average for the summer months lies exactly in the preferred temperature range of the larvae, that the average of the spring, summer, and fall months together, which constitute the months of chief activity of the larvae, is at a temperature at which the animals remain

normally active, and that the averages for the winter months do not drop below zero. This aspect is important when we compare with these data the observations concerning the annual activity rhythm (Chapter C III 1a).

By way of summary of this chapter on ecological factors it may be stated that the interaction and interplay of the various factors discussed here have a great importance in the life of the larvae: The special choice of subsoil, negative phototaxis, scototaxis, thigmotaxis, hydrotaxis, lack of protective mechanisms against desiccation keep the creatures in an environment to which their morphologico-anatomic and physiological qualities are adapted, namely in a humid, even-temperatured biotope whose microclimate exhibits no great extremes in any respect.

II. Data Concerning the Developmental Cycle

In order to have enough material, I had to grow the insects myself. The following data on the developmental cycle thus originated as a mere by-product of my work.

The conjectures in the literature that our native lampyridae as a rule have a one-year developmental cycle (Acloque [1], Newport [95], Vogel [129]) were opposed by others (Höllrigl [62], Main [79], Rogerson ["On the Glowworm," Philosophical Magazine, Vol 58, 1821, page 53], Verhoeff [126]) that postulated a two-year cycle. For non-European lampyridae, Hess [58] assumes for Photinus consanguineus, Photinus scintillans, Pyropyga fenestralis, and "most other native (= American) fireflies" a two-year cycle, while Hutson and Austin have demonstrated a one-year period of development for the Indian firefly Lamprophorus tenebrosus.

Except for the last-mentioned finding, no one seems to have succeeded up to now in raising lampyridae from egg to imago, for the authors base their statements on the developmental cycle solely on indirect observations. Thus the authors that have made up their minds in favor of a two-year developmental cycle adduce the fact that in larvae found during the pupation period a definite two-phase difference in size may be observed. For a one-year cycle I have found neither supporting data nor arguments for successful raising within that time.

These contradictions, because of the too small number of experiments and observations up to now, are based on only a few individual insects.

The differing and uncertain statements concerning the developmental cycle, the obvious difficulties in growing the larvae, and my desire to obtain as many adult individuals from my breeding operations caused me to begin on a large scale. I began with 4289 Lampyris eggs, which hatched into larvae with very small losses (page 38). In the case of Phausis splendidula I tried growing from the egg less intensively, because I assumed I could get enough imagines, as both sexual forms of this species luminesce quite visibly. -- On the basis of this extensive insect material I can make quite sure statements about the life history and habits of my insects.

1. Egg-Laying and Layings of Eggs

Females that are bred toward the end of their short lifetime lay the eggs immediately after copulation if they are in almost natural environmental conditions. The sooner after the female's emergence as an imago that a copulation takes place, the longer it may be before the egg-laying. This fact is also deducible from a variety of observations in the open. The egg-laying may occur 6 to 8 days after copulation if the female copulates immediately after emerging from the pupal state. This extreme case, to be sure, may not occur in nature, since the female as a rule remains inactive for a certain length of time after shedding the skin (see below). This is probably causally connected with the maturation of the eggs. In dissecting freshly hatched females — and for comparison older females — I was able to satisfy myself that the eggs are in very different stages of development depending on the time of the imaginal molting. It is true that there are normal-sized eggs immediately after the shedding of the skin, but a large part (especially in the distal end of the ovarial pouch) are considerably smaller. This condition changes progressively, though not always in the same time relation with the imaginal shedding of skin, until all the eggs reach a certain size and are ready for laying, after about five days on the average. In most cases the eggs are layed after 1 to 3 days at night, only occasionally in the daytime.

The eggs are deposited at special places. If there is a possibility of choosing between dry and damp ground, the damper is preferred, and in the same way well covered ground is preferred over open, uncovered ground. In the open the female does not travel very far between copulation and egg-laying, but lays the eggs in the immediate vicinity of her habitual place to shine every evening or in the place where she hides in the daytime. As a rule the places chosen are well protected places in the grass-root mat very close to the ground, in cracks of stones, under stones, in coarsely friable earth, on the underside of the leaves of small ground plants (e.g. mosses), — in other words always as close as possible to the zone of contact of earth and plants, but not actually underground.

After mating the female as a rule no longer appears in the evening in typical glowing position, nor does she any longer glow. An exception to this is found in Lampyris females which (under laboratory conditions) are brought together with a male immediately after shedding the skin. These females lay only a few eggs, either immediately or after a day or two, and then again exhibit complete sexual appetency behavior (which see). Then after repeated copulation all the eggs are laid. This behavior points to the abovementioned increasing maturation of the eggs after the shedding of the skin; in addition it seems that the spermatozoa cannot be visibly stored for several days. The female goes about very slowly, almost searching, often with the ovipositor slightly outthrust, then with boring, searching motions pushes the fully extended laying apparatus into a crack in the ground or, with downward curving abdomen, under a moss leaf or root fiber (Figure 23). The eggs are thus laid

GRAPHIC NOT REPRODUCIBLE

Figure 23. Lampyris female laying eggs. (above)

Figure 24 (right). Batch of Lampyris eggs laid at one time (about 7 x).

singly, though in fairly large number in favorable places, otherwise scattered, but in the normal case never hanging together in clumps (Figure 24). To each egg that is laid is added a drop of viscous, sticky, colorless liquid that fixes the egg to the surface it rests on. This adhesive drop may immediately precede the emerging egg or be secreted simultaneously with the egg. In both cases it immediately surrounds the egg and may have 1/3 to 1/2 the volume of the egg. With a certain skill and caution and with knowledge of the approximate chronological sequence of the emergence of the eggs, egg-laying can also be experimentally induced in the female that is ready to lay, by stroking the abdomen of the insect from front to back with a gentle pressure. During the 2 to 3 day duration of the egg-laying the plump mature female visibly decreases in volume, and at last is paper thin when she has laid all the eggs. After the egg-laying the females die after a varying length of time. All females were dissected post mortem to determine the exact number of eggs, for not all eggs were laid in all cases before the death of the insect (not even in the open). While it is often small, obviously immature (citron colored) eggs that are found post-mortally in the ovaries, that is not an invariable rule, for often eggs of normal size and obviously mature (light orange) are found. In 62.4% of 46 accurately checked cases all the eggs were laid, and most of the other females contained only one to three eggs. The cases in which only 10 to 30 fertile eggs were laid must have been anomalous because death occurred prematurely. Normally a laying consists of 60 to 90 eggs (average of over a hundred layings in the open and under cultivation); only occasionally are layings of a little over a hundred eggs encountered. Reports in the literature of hundreds of eggs (Kuhnt [70], Kaiser ["The Luminescence of Lampyris splendidula L.," Anzeiger der Akademie der Wissenschaften, Wien (Informer of the Academy of Sciences, Vienna), Vol 17, pages 133-134, 1884]) cannot be correct. The absolute number may fluctuate considerably: 41 at the minimum, 198 at the maximum (all immature, often tiny eggs counted in). It may be conjectured that this difference is correlated with the difference in size of

the females, but I can give no exact information about this. In any case in the outdoors quite viable females of 12 mm may be found along with gigantic females of 30 mm, though the extremes are to be regarded as exceptions; on the average the females would be about 20 mm long. Each of the paired ovaries produces about the same number of eggs.

The freshly laid eggs are spherical, with a diameter of 1.0 to 1.3 mm, untransparent and light orange in color. (The rather large eggs fill the mature female's entire body cavity right up into the prothorax.) The skin of the egg is at first so soft that at a touch or an effort to move the egg from the surface it rests on the egg breaks and runs. After only about 12 to 24 hours the eggs become quite considerably harder (probably depending on the atmospheric humidity). The surface of the egg is not entirely smooth, but appears under 150 to 200-fold magnification to be marked irregularly with flattish elevations and depressions.

That the eggs are quite sensitive is shown by accidental observations of neglected layings. In dried-out culture vessels the eggs show shrunken places caused by loss of water; even the hardest egg skin is thus no absolute protection against drying. But since in the natural biotope the eggs, in view of the high atmospheric humidity there (see pages 19 ff.), do not dry out, no special provisions need to be at hand. If after visible loss of water the eggs are placed in a high humidity, the shrunken places disappear again through absorption of water and under favorable circumstances the development of the eggs may be successfully completed, sometimes with a delay in the time of hatching.

A great controversial question in the literature is the question of whether the eggs are luminescent or not. The answer to this question is often represented as decisive in the matter of whether the process of luminescence is to be regarded as purely a luminescence of the species itself or whether it may be considered as conditioned by symbiontic luminescent bacteria. (For further discussion of the symbiosis problem see Chapter E I 3.)

De Bellesme [6], Bongardt [10], Dubois [35], Fabre [40], Gerretsen [45], Hess [58], Höllrigl [62], Hutson and Austin [63], Knauer [68], Kuhnt [70], Main [79], Verhoeff [126], Vogel [128,131], and Wielowiejski [140] have observed a luminescence. Czepa [32], Haupt [57], Meissner [90], Newport [95], and Weitlaner [137] do not believe that the eggs themselves are luminescent or note expressly that they have never observed it. Even among those who affirm the luminescence there are opinions that do not assume any inherent luminescence of the eggs, but rather that the eggs are smeared with a luminescent substance.

In the many eggs (fertilized and unfertilized, about 6000 all told) that I was able to observe in the course of my investigations I established the luminescent capacity not only in eggs laid in the natural way but also in eggs found in the body cavity of mated and unmated females whose luminous organs had remained entirely undamaged , as well as in externally sterilized eggs of

mated and unmated females. (External sterilization by a five-minute bath in 10% solution of chloramine in alcohol, as recommended by Fink, Zeitschrift für die Morphologie und Ökologie der Tiere (Journal of Animal Morphology and Ecology), Vol 41, 1952, page 78, or in a five-minute bath of 2% quinosol solution as recommended by Nordgren and Funkquist, Nordisk Hygienisk Tidskrift (Scandinavian Journal of Hygiene), Vol 21, 1941, pages 269-294.) The luminescence of the eggs is therefore an inherent luminescence (Figure 25). Contrary to various opinions that the eggs glow only at certain periods of their development, I was able to establish luminescence throughout the entire period of egg and embryo development. At first -- whether inside or outside the female body -- there is a weak phosphorescent glow distributed over the whole egg, while in about the last quarter of the embryonic development the glow is concentrated more in a definite place and is similar to the light of the larva. Probably at that time the "luminous organ" is identical to that of the hatched larva. The glow of the eggs can be intensified by mechanical stimulation.

Figure 25. Externally sterilized eggs taken from an unmated female (Lampyris), photographed in their own light. (About 8 x.)

It must also be mentioned that unmated females show a quite different behavior in egg-laying. The sexual appetency behavior appears greatly heightened (cf. Chapter D I 1 b), while the eggs as a rule are retained until shortly before the natural death. (This is also observed in the natural habitat.) The unfertilized eggs, which do not differ externally from fertilized ones, are then expelled premortally, either by repeated efforts and in clumps, or else in one single convulsive squeeze, after which death usually occurs immediately (Figure 26). Almost always a more or less large part of the eggs are left in the ovaries; only rarely are no eggs laid at all. Apart from the clumpy configuration infertile batches of eggs may be recognized by the fact that the egg skins do not harden; the eggs do not adhere firmly to the surface on which they are resting, like the fertilized ones, and occasionally they shrink a little, take on a dark orange coloration, and putrefy or grow mouldy, depending on conditions in the vessel, in a varying length of time (usually within one to three weeks). It is to be assumed that the liquid secreted in ordinary egg-laying is not given off with unfertilized eggs, and that that liquid has not only adhesive but also protective functions, against mechanical

Figure 26. Egg-laying unmated female (Phausis), shortly before death.

and infectious damage. "Fertilized" eggs (= eggs with solidified egg cases) in which no development into the larva takes place will keep up to a year according to my observations (perhaps even longer) without putrefying or becoming moldy.

The processes described for Lampyris are very similar in Phausis. Time, place, duration, and manner of egg-laying are as in Lampyris. One difference is that there is not as high a degree of willingness to lay eggs in captivity; unmated females often die with their entire stock of eggs. In egg-laying a spasmodic, powerful contraction of the abdomen both lengthwise and in the dorsiventral direction is noticeable, which pushes an egg into the vagina and finally ejects it. With suitable lighting these processes can be followed clearly. Otherwise the behavior is the same as in Lampyris. The size of the eggs is about 0.6-0.8 mm; the eggs have a somewhat lighter color than Lampyris eggs. A laying consists on the average of 60-90 eggs; the absolute number is 57-147 eggs (in 34 dissected females). As to luminescence of the eggs, what has been said of Lampyris holds here too.

2. Embryonic and Post-Embryonic Development

I did not study the embryonic development myself, and shall describe here only the visible processes. The opaque eggs, at first light orange in color, do not increase in size in the course of developemnt, as described by Newport. The rigid chorion, too, seems to oppose any increase in volume. Besides the changes in the luminescence of the eggs noted earlier, a change in the coloration of the egg and in the inner structure makes itself evident. Toward the end of the egg development, inside the egg, which is becoming only a little more transparent, a separation of the egg mass sets in; a light orange peripheral strip (probably the developing embryo) surrounds a lighter central portion (probably nutrient material). At about this time the diffuse luminescence of the whole egg changes into a concentrated point-like glow at a spot not precisely determinable. The time taken by the development must be, as in all insects, dependent on external factors, especially on temperature and humidity. Thus in the case described on page 36 part of the eggs laid on 14 July 1957 hatched on 20 October and on 21 November 1957, or after 99 and 131 days respectively. The rest of the batch were no longer capable of developing. At an average temperature of 18-20° C and about 80-100% relative humidity the larvae hatch more or less constantly after 35.3 days (average of 46 layings). It must be borne in mind that not all eggs are laid on one day simultaneously and neither do they hatch at the same time; the period of hatching may extend over 8 days. In most reports the time is reckoned from beginning of laying until the hatching of at least 75% of the eggs. Under suitable conditions, adjusted to those of the natural environment, mortality is very low; from 4289 eggs 3967 larvae hatched, the mortality thus being 7.5% on the average. In many layings the hatching rate was 100%. The percentage was reduced to 92.5% only by a few batches that for some reason developed badly. With the above-mentioned exception all the layings had hatched by the end of September. Newport's assumption of a two-year developmental period only in the case of larvae that hatch out too late in the season, but normally

only a one-year one, is not tenable according to my experience. During the rest of the year the larvae reach a uniform or not greatly differing size of about 6-8 mm, as a rule without shedding the skin (cf. pages 40 ff.).

At the time of the hatching the chorion is burst in an irregular crack and the waxy white larva, unpigmented except for the eyes, makes its appearance without further effort. Hatching takes place predominantly at night, but occasionally, on dark, overcast days, in the daytime. The integument of the young, freshly-hatched Lampyris larvae, up to 4 mm in length, darkens within seven hours, and they are then quite like the older larvae, even in external appearance. Immediately after leaving the egg sheath and during the period when pigmentation is acquired the larva if undisturbed is inactive and assumes a position on its side, curled in a semicircle. Afterwards, even in the first few days, it is very active and takes nourishment.

In the young larvae during growth and after sheddings of the skin until the final stage it is hardly possible to observe externally any characteristic progressive change. No measurements of the cephalic capsule are possible in the living animals, since at the slightest touch or breath of air they retract the head completely; measurements of length give extremely variable results depending on state of nutrition, and are also inaccurate because of the possibility of a telescoping contraction of the abdomen. I did not succeed at the time in finding any narcosis not dangerous to life that would for example have permitted measurement of the cephalic capsule. The only possibility of identifying definite early stages seemed to me to be in the nature and development of the hairs or bristles, but exact comparative studies of that matter lay too far outside my actual field of investigation.

If we compare the chronological sequence of moltings of the larvae from several layings (A-G) it is conspicuous that they take place in each case approximately simultaneously. (Cf. time of appearance.) Examples:

Laying	A	B	C	D	E	F	G
First Series	February e.g. 14, 18,23,26, 27	February e.g. 10, 11, 17	February e.g. 10, 13,15,17, 24	February e.g. 21, 28, and 2 March	February e.g. 18, 20,23,27	February 13,15, 22, and 1 March	February 15,19,25
	several larvae molted on one day in each case						
Second Series	June (10,19)	May (20,26)	May-June (20 May, 1-2 June)	June (2,6)	June (7)	May (26)	May-June (26 May, 4 June)
	in some cases several larvae molted on one day						
Third Series	July (4)	July (4,8,18)	July (7)	July (4)	+ 14 June	July (12)	July (27)
	only occasionally more than 1 larva molted on one day						
Fourth Series	+23-24 August	August (26) +15 Sept.	+16 Nov.	Sept. (5) +25 Sept.	—	-10 Sept.	-17 Sept.

+ Process completed for laying in question on date shown.

These data are for broods that were kept at 18-20° C even during the winter half of the year. In scattered cases the larvae molted as early as the beginning of December, before their winter pause in activity (Chapter C III 1 a). Under outdoor conditions the larvae do not molt in the same year that they leave the eggs. In the outdoors the first molting begins somewhat later than shown on the above table. It is found, however, that in an observation period of more than a year the molting periods within one laying vary little, and that even in several layings (under approximately similar conditions) they remain fairly synchronous. Comparative and supplementary material from outdoors permits the conclusion that the abovementioned molting periods all shift somewhat toward the end of the year, so that the first molting takes place soon after the winter rest (March-April); the second and third by preference coincide with the months of most active food-seeking on the part of the larvae (July, August, September or October). In year-old and mature larvae one molting place in the late spring and one or two (depending on food conditions) in the fall until the pupal molting in May or in June. In the last year of their larval period (i.e. before pupation) I was able to find a molting only in exceptional cases, so that a total of only four to a maximum of six moltings are to be reckoned with in the larval period. This relatively small number of moltings over a 33-34 month larval period with a growth in length by a factor of 5 to 9 and approximately a six-fold growth in breadth can be very well compensated for by the larva through great stretching of the intersegmental skins between the segments on the one hand and the tergites, pleura, and sternites on the other.

The molting is preceded by a three to six-day rest period, during which the larva usually moves only in response to mechanical or light stimuli. It lies on its back or side in a place protected from the light, with abdomen curved ventrally into a semicircle, until leaving the exuvia. That the larvae burrow into the ground for molting I was never able to observe, although they had a chance to do so (sandy soil, mold humus). Phausis larvae do make themselves a hole under leaves and the like, of circular to oval outline, as described in connection with the pupal molting (Figure 27). In rare cases larvae were observed that molted in snail shells that they had previously eaten empty. A day or two before molting the larva pulls its head back from the cephalic capsule into the prothoracic cavity. (The empty cephalic capsule, usually bent in the ventral direction, can be removed without injury.) At about the same time it is possible to see the contours of the larva in its new integument through the intersegmental membranes. Immediately before the bursting of the old integument the exuvial part of the last two or three segments of the abdomen is pulled off to the rear and hangs slack and empty.

Figure 27. Molting chamber (opened) of a Phausis larva. The chamber is made by means of the mouth parts and the prothoracic shield.

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Figure 28. Larval molting. (Lampyris)

The exuvial integument is tightly stretched over the rest of the body, but seems to have little contact with it, since the divisions between the segments in the old and the new integument are not in line. The anterior end is subjected to the greatest pressure shortly before the molting, for at this stage quite a slight pressure from outside on the prothorax often suffices to cause the skin to burst open. The integument bursts, not on the dorsal median as in many other insect larvae, but in a transverse break at the upper end of the prothoracic segment, through which the nearly unpigmented head appears. In the course of thrusting forward movements of the larva to free itself, by contraction and stretching lengthwise and by movements of its anterior end, the transverse slit is first widened laterally on both sides to the posterior corners of the prothorax. At the time that parts of the forelegs become visible the integument tears further -- probably because of bracing actions of the legs -- in the caudal direction along the pleuron-tergite line to the metathoracic segment, and occasionally as far as the first abdominal segment (Figure 28). Under this big cover, not by leg movements, but by alternate contraction and stretching of the abdomen, the larva pushes itself out of the exuvia or pushes the exuvia to the rear, presumably with the help of certain large anally oriented setae situated on both sides at the posterior corners of the second to eighth abdominal sternites and with the further help of the pygopodium, which is already capable of functioning. After molting is completed the unpigmented larva (if undisturbed) lies almost motionless on its side for several hours, except for occasional violent movements of the head, in which the head and the parts of the neck important in capture of prey (according to Vogel parts of the prothorax and the cephalic capsule) are stretched forward to their maximum capacity; in the same way the pygopodium is extended to its maximum capacity and retracted. Since the larva frequently takes rests of varying duration during the molting process, the duration of molting cannot be easily stated. Normally it can be completed in two to four hours. It takes place at night or on dark, overcast days, in the latter case usually in the morning or evening hours. In the normally molted larva the legs are practically incapable of movement, stiffly stretched toward the rear, for about five or six hours. After that, normal movement is possible, but the larva if undis-

turbed remains inactive for about twelve hours. Not infrequently a molting miscarries, and this may happen at quite varied stages of the molting process. Thus e.g. the outer, old integument may be already loosened from the new one, the head retracted, and the last abdominal segments of the exuvia already empty, and still the larva is unable by efforts over several days to break the skin. It also happens that the exuvia does not burst at the right place. In all these cases the unsuccessful attempt at molting ends with the death of the larva. In only two cases was I able to observe that a larva had freed its head and legs from the exuvia (in one case with my help) and that the relatively long abdomen still remained in the old integument. The two larvae survived; the free exuvial parts broke off in the course of time, and the abdominal exuvial part burst -- especially in the intersegmental membranes (movements, expansion) -- and was cast off at the next molting. -- Deformities occur in the larvae from poorly molted appendages, especially mouth parts and legs. Cases in which the mandibles, feelers, or antennae are badly deformed end in the death (starvation?) of the larvae.

The freshly molted larva is almost colorless with the exception of the heavily chitinized mouth parts and the ocelli. The tergites, sternites, and pleura in particular, however, very rapidly take on first a light gray and then gradually the final dirty dark gray coloration after about 24 hours. A freshly molted larva can still be distinguished from others for days (especially by the strikingly pink posterior corners of its tergites and by the lighter, flesh-colored or livid white connective membranes between tergites, sternites, and pleura).

Fig. 29. Molting into the pupa (Lampyris male pupa).

Molting into the pupa occurs in the same way as larval molting (Figure 29). It is preceded by a rest period of 8 to 20 days during which the larva assumes the same position as in the case of a larval molting. The time of molting is dependent on the local climate. Near Mainz the larvae pupate usually in May; in the harsher climate of the Palatine forest pupation usually does not take place until June or even in July, in extreme cases not until September, as I deduce from the late appearance of the Lampyris females. With higher temperature (room temperature) and artificially curtailed winter I was able to get pupae as early as March.

Pupation also occurs in places protected from light. The pupa is capable

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Figure 30. Pupation chamber of Phausis (opened); male pupa and larval exuvia.

of quite considerable movements, in fact even of "locomotion." Through the very thin, transparent pupal exuvia an increasing darkening of the at first waxy white imago may be seen, but this does not reach its climax until shortly before the molting into the imago. The duration of the pupal period (not counting the preceding rest period) differs between the sexes. The males require at 20° C from one to three days longer; this may be conditioned by the complicated morphological development of the males (wings, eyes). The females of Lampyris take 10-11 days before the imaginal molting, the males on the average 13 days. -- In Phausis the pupal stage lasts 7 days on the average and occurs in the same way as in Lampyris, but with the difference that the larva makes itself a hemispherical pupation chamber of about 10 mm diameter, open at the top, under a leaf, bit of wood, or the like (Figure 30). Also the increasing pigmentation can only be seen in the eyes (the pigmentation of the male imagines sets in only after the imaginal molting; the females remain unpigmented throughout life).

In the pupal stage the well-known sexual dimorphism shows up for the first time (Figures 31a,b).

Figure 31a. Sexual dimorphism of Lampyris pupae (female left, male right).
Figure 31b. Sexual dimorphism of Phausis pupae (male left, female right).

The molting into the imago is relatively quickly completed (often within a few minutes), with very active participation of the legs and the abdomen, and takes place for the

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32a

32b

32c

Figure 32a. Molting into the imago (Lampyris male).
Figure 32b. Molting into the imago (Lampyris female).
Figure 32c. Pupal exuvia of a Phausis female.

most part in the late evening or at night. The pupal skin of the Lampyris female opens as in the larval molting already described. In the males of both species and in the Phausis female it bursts along a preformed dorsal median line from the anterior edge of the prothorax to the first and often to the second abdominal segment. This crack usually does not tear laterally to both sides at the caudal end to form the T-shaped molting opening characteristic of many beetles (Figures 32a,b,c). Molting to the imago miscarries more often than that to the pupa. The thin skin occasionally tears in a transverse tear between thorax and abdomen; the insect, left to itself, is then only able to shed the posterior part and often dies prematurely. I was never able to observe appetency behavior, copulation, or egg-laying in such insects. Males with wings not fully extended, stunted, incapable of flight exhibit (as has also been observed outdoors) a suggestion of appetency behavior, find females, and are normally capable of copulation.

The appearance and disappearance of the imagines is also climate-conditioned. The imagines of both species appear approximately simultaneously in one biotope, but the whole period of appearance is over sooner in Phausis than in Lampyris (Phausis toward the end of July, Lampyris until September). The main time for both species is June and the first half of July. According to my observations and those of other authors (Höllrigl [62], Knauer [68], Verhoeff [126]) the main period of appearance of the two species coincides chronologic-

ally. According to Bongardt [9,10] and Macaire [76] Phausis appears later than Lampyris (according to Bongardt by three weeks!). In a four-year period of observation I found that almost all imagines (especially in the case of Phausis) appear suddenly in a biotope for eight to fourteen days and then disappear; very rarely is there a second period of appearance. I could not afford to miss these main periods of appearance and flight if I wished to have enough specimens for my studies of reproduction. The cause of the sudden appearance of the imagines within one biotope may lie in the nearly synchronous moltings under the same environmental conditions, for it is a striking fact that what has been said is particularly true of the smaller biotopes (of up to about 150 square meters). This also applies to Lampyris, though with somewhat extended time limits.

The numerical ratio of males to females is different for the two species. For Lampyris, since the males do not glow, I must rely solely on experience in growing the insects. For each male there were three females (18:54). For Phausis I can give no precise statement in view of the small number that I grew myself. The ratio was almost 1:1 (18 males to 15 females). But since in this case both sexes glow, it is possible to get some idea out of doors. There the ratio shifts very much in favor of the males, about 5 or 6:1 (88:16). Toward the end of the seasonal period of appearance the sex ratio of both species shifts surprisingly; males become increasingly rarer, so that females hatching late in the season often remain unmated in spite of complete appetency behavior.

Because of the importance of the sexual characteristics in the reproduction process, let us summarize them briefly here.

Males of both species: Normal beetles with wings and elytra, large eyes (of complex structure; see Chapter D I 3), long, hairy antennae; in the Lampyris female [sic; surely we are to read "male" here] the larval luminous organs persist, but are concealed by pigment, while Phausis has two well-developed, functioning imaginal luminous plates ventrally in the sixth and seventh abdominal segments besides the pigment-concealed larval organs [see Note]; smaller body size, especially in the case of Lampyris.

[Note] The larval luminous organs of Lampyris consist of one bulbous process on each side in the eighth abdominal segment. In Phausis these larval luminous organs are found laterally in variable arrangement within the species from the second to the sixth abdominal segment as luminous bulbs, odd or even in number. Within the individual, however, the arrangement remains constant through successive moltings. The number of luminous points

varies from three to twelve, but most often six are found, i.e. three pair of luminous bulbs. The larval luminous organs remain capable of function throughout all post-embryonic stages of development (but hidden in males of both species). The imaginal luminous plates of the females (and of the Phausis males) become active about three to five days before the molting to the imago (Figure 38a-e).

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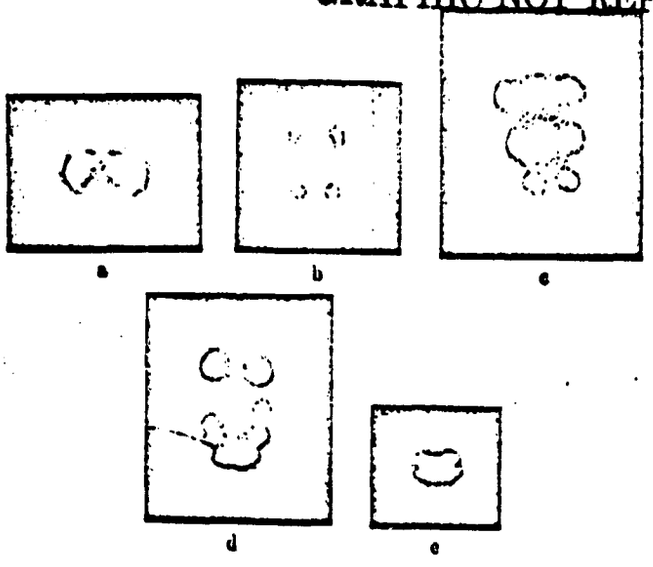

Figure 33 a-3. Luminous organs of the luminescing stages of Lampyris and Phausis (photographed in their own light). a)Lampyris larva; b) Phausis larva; c) Lampyris female; d) Phausis female; e) Phausis male.

Females of the two species: Small eyes, wingless (in Phausis rudimentary elytra, incable of function), shorter, less hairy antennae. In both species besides the functioning larval organs imaginal luminous plates ventrally in the sixth and seventh abdominal segments. Lampyris females are as a rule larger than the males, of clumsy, not well articulated build. The larva-like females are almost sedentary and very sluggish, while the males are typical very mobile beetle imagines.

The lifetime of the imagines is relatively short and serves solely for reproduction. (Cf. the question of intake of nourishment by the imagines, Chapter E II 1.) Immediately after the imaginal molting copulation can take place, and after a more or less complete egg-laying the females die. The males live about as long. From outdoor observations and under artificial growing conditions this period is found to be for Lampyris males and females about 10-18 days (11 males averaged 12.7, 22 females 14.5 days at a constant 20° C),

for Phausis females 7-10 days, for Phausis males only about 5-7 days. Under outdoor conditions the lifetime of the males of both species is often about 1/4 shorter than these figures. The lifetime can be extended by preventing copulation and by low temperature (e.g. 10° C), in Lampyris females up to ten days, in Lampyris males only about three days. In Phausis the lifetime can hardly be lengthened significantly. The conditions mentioned on page 34 in connection with egg-laying play an essential rôle in determining the life span. Thus e.g. (in the Lampyris female) the lifetime may be reduced by immediate copulation after the imaginal molting (only under artificial conditions), early egg-laying, and early death (to only 5 to 7 days). Similarly the life of a male that copulates often is shortened.

Approaching death is intimated by similar aging phenomena in both sexes. About 1 to 2 days before death the insects show locomotor movements only in response to mechanical stimuli; movement then is awkward, sometimes more or less uncoordinated; the insects often fall over and remain lying on their sides or backs without making the turning movements that otherwise occur immediately. In the males aging manifests itself in diminished inclination to fly. Shortly before death the insects are usually found lying on their sides or backs with extremities intertwined, the tip of the abdomen curled ventrally up to the thorax. Unmated females, which have ejected a clump of eggs premortally, presumably are usually fixed in that position with the sticky eggs. -- As a rule the luminous organs glow premortally and for several hours postmortally. Males and females of Phausis not uncommonly bury themselves before death, but I have never observed that in Lampyris.

We shall discuss here only the luminescence which occurs under natural circumstances in the life of the larvae and pupae, and not that induced by unnatural influences (for which see the physiological literature mentioned in the introduction, which is preëminently, though in many points contradictory, a physiology of the luminous organs). The diurnal distribution of the periods of luminescence will not be taken up until Chapter C III 1.

It should be stated at the outstart that the luminescence of all post-embryonic developmental stages is limited to the definitely circumscribed luminous organs and not, as Czepa [32], Macaire [76], Meissner [92], Verhoeff [126], and Weitlaner [137] state, distributed all over the body (on this point cf. Figures 33 a-e and 79-81).

Lampyris larvae do not glow continuously. Bongardt assumes on the basis of superficial experiments that luminescence

once begun continues, whether the insect is willing or not. Vogel's observation that the larvae glow continuously during the months of the winter rest is not valid, either. Normally (i.e. outside of the larval or pre-pupal rest periods) the larvae glow at completely uncontrollable variable intervals, without visible external cause (cf. Figure 38). Even the most powerful mechanical stimuli are incapable of inducing a glow. The duration of luminescence varies from one second up to minutes. Frequently the pattern of the luminescence of Lampyris larvae is that their light lasts for about 4 seconds, reaching a maximum intensity by about the end of the first quarter, holding that maximum for about another quarter of the total duration, and then gradually decreasing in intensity until it is totally extinguished. The beginning and end of this "lightning" appear to be voluntary. This is also supported by the fact that when a larva that has just begun to glow is touched the glow immediately ceases (not always conditioned by the fact that the larva falls down from fright at a touch, so that the ventrally located luminous organs become invisible, but the luminescence, as Bongardt believes, still continues).

On the luminescence of Phausis larvae there are only a few observations (Höllrigl, Verhoeff), but they are all to the effect that Phausis is disinclined to glow without external cause, such as fright or contact. I caught the several hundred Phausis Larvae by making use of this peculiarity. The larvae also react to loud noises (e.g. of blank cartridges). If they are stimulated repeatedly within a few minutes, as a rule the luminescence fails to occur. As Figure 38b shows, however, they too glow voluntarily. The duration of luminescence is commonly longer, but just as variable as in Lampyris larvae, but it increases in intensity up to a maximum often held for minutes at a time and then decreases to total extinction of the light.

The larvae of both species behave like the Phausis larvae during the molting rest period and the winter rest period, during the state of rest before pupation, and during the pupal period, but with the difference that they light up very intensively after every stimulus, no matter at what interval the stimulus is given. It can even be brought about that pupae or larvae in that condition glow continuously for a fairly long time with a slight continuous stimulus. It is probably to this that the description of continuously glowing pupae is to be attributed (Meissner and others), since merely breathing or moving around a table not secured against shaking will provide such a continuous stimulus. Occasionally larvae in a condition of satiety react similarly to such stimuli. This

luminescence occurring under specific physiological circumstances can also be induced at any time in daylight or under artificial lighting. The many contradictory findings of other authors are very probably to be attributed largely to this circumstance.

3. Raising Fireflies and Its Results

In the literature there are no reports of successful raising of Lampyris or Phausis larvae from egg to imago. I attempted raising them in glass dishes (5 cm high and 10 cm in diameter, which were covered with glass plates and the bottom of which was lined to a depth of 1.5 cm with a layer of gypsum which when filled with distilled water provided for a long-lasting uniformly high atmospheric humidity in the vessel.

Large-scale raising was started within a year (from over 4000 eggs). Plant and animal pests (Chapter E I 2), feeding difficulties, molting crises, the attempt to accelerate development without a winter rest period at a high room temperature (20° C) all year round, and other unfavorably chosen ecological conditions are largely responsible for the high mortality. (Only 60% of the insects lived from September to December, 7% until February, 2% until April.) The animals grown in this way were on the average larger than those of the same age under outdoor conditions. Of the animals grown in this attempt of course none were used for experimental purposes.

After this failure I investigated the various ecological factors (Chapter C 1) and arranged the growing vessels in accordance with the findings obtained and with previous knowledge. The gypsum bottom was replaced with sand, which could be more easily kept clean and more easily changed, so that hiding places for pests were considerably reduced; the larvae were given a little forest ground litter for cover (leaf litter for Lampyris, mainly raw humus for Phausis); the growing vessels were also protected from direct sunlight and always kept moist; a winter rest period of at least one month at 0-5° C was observed (cf. Chapter C III 1 a). The greatest difficulty in raising them from the egg is feeding the greedy young larvae with correspondingly small snails, up to about 3 or at most 5 mm in length (or in shell diameter, in the case of shelled snails), which incidentally renders necessary the raising of snails, not easy in itself. In the slime of a snail that was too big for them but had been attacked anyway, or on pieces of snail put into their vessels, dozens of larvae had often gotten stuck overnight and presumably suffocated. Losses at molting and from the attack of pests were unavoidable.

Because of the long period of development the renewed effort to grow the insects from the egg has not yet been completed, but after the first year it is running much more successfully. (19% of the larvae are still living.) The supplementary data on the developmental cycle and particularly on its duration I obtained on the basis of about 600 Lampyris and about 400 Phausis larvae and imagines that I have obtained from outdoors in the course of the years. These were for the most part from year-old to mature larvae, most of which I brought through to imagines. I have thus had one-year larvae under conditions of cultivation for far over a year, and because of the difficulty of obtaining Lampyris males I am concentrating my interest entirely on these raising attempts. At least with them there were no feeding difficulties, though there have been serious losses because of pests and during molting crises. Although so far I have not succeeded in raising the insects continuously from egg to imago, I have been able to follow the entire developmental cycle in two stages.

That great losses must also occur under natural outdoor conditions in their habitat may be shown indirectly by the following observation: I completely wiped out a small, well-defined Lampyris biotope of about 30 m^2 by taking away all the larvae and imagines during a continuous check extending over three years. During the first year I found 6 females. (They were all the females of that period, for no new generation would be found.) If we assume that all six females stem from one average laying (75 eggs), the loss would be 84% (an equal number of developing males reckoned in; cf. page 45). During the period of appearance of the sexual forms in the second year no females were observed (in the case of Lampyris, males cannot be checked). Meanwhile I had presumably caught all the larvae, for in the third year I found none. There were a total of 56 year-old to mature larvae. This number, too, shows the great losses during development in the natural habitat. For Phausis the losses may be estimated as lower.

This thorough investigation of this habitat permits conclusions as to the length of the larval period and so as to the total duration of the developmental cycle. Comparison of the developmental stages of larvae that can be found at one and the same time (in April! -- Figure 34a, I-III) shows clearly three well-differentiated size classes: 34a I is of the same size as the animals I grew after 8 months, 34a II is a 20-month-old larva that still did not develop into the imago that same year, and 34a III is a 32-month-old mature larva, which pupated in May. A further indication of three-time wintering of the larvae is given by the fact that in September and October I found lampyris larvae that in point of size were

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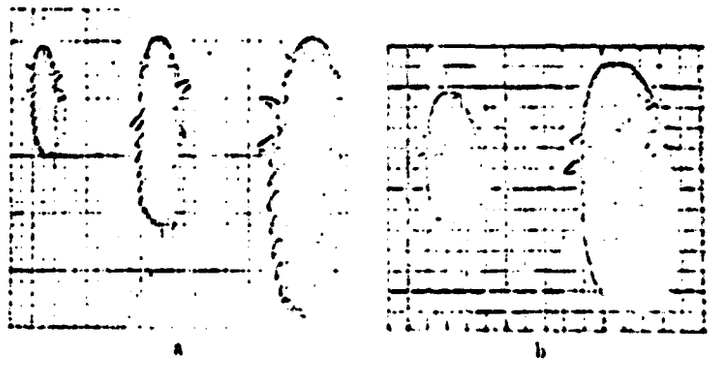

Figure 34a. Three Lampyris larval stages (I-III) found at the same time outdoors before the pupation season (April). I - one-year-old; II - two-year-old; III - three-year-old larva (on millimeter-ruled paper).

Figure 34b. Two Phausis larvae found at the same time in November (after the time of appearance of the sexual forms). Left: one-year-old larva, right: two-year-old larva, which pupates the next summer (on millimeter-ruled paper).

full-grown, but had not developed into imagines in the summer just past and lived through another winter. In this case the larvae (also according to my laboratory findings) could only have been of the stage represented in Figure 34a (II), which did not become sexual forms until the following spring.

Everything would seem to tell in favor of a three-year cycle in Lampyris (with the larvae living through three winters and thus reaching an age of 2 2/3 years). The situation is similar with Phausis; though in this case I have only conducted the raising from the egg for a few months, the laboratory observations on older larval stages in connection with outdoor observations show a three-year cycle here, too (Figure 34b).

The table on the next page summarizes the findings from growing experiments and outdoor observations for Lampyris.

Table 13 [sic; cf. page 30]

Egg	Embryonic development	30-35 days
Larval Stage	To 1st molting	7-8 months (+ 1st winter rest period)
	To 2nd molting	4 months
	(To 3rd molting)	2-3 months
	To 4th molting	6-7 months (+ 2nd winter rest period)
	To 5th molting	4 months
	To 6th molting	2-3 months
	To pupal molting	7-9 months (+ 3rd winter rest period)
	Total larval period	about 33-34 months
Pupal Stage	Pupal period (male and female)	9 days
Imaginal Stage	♂ adult period	10-16 days
	♀ adult period (mated)	10-16 days
	Time before egg-laying	up to 13 days
	Period of egg-laying	as a rule, 2-3 days
	Time after egg-laying	as a rule, 1-3 days
	Total duration of life cycle	about 33-34 months

III. Biology of the Larva

1. Phenology

With regard to the annual rhythm of larvae of the Lampyridae the opinions of different authors are divergent: according to Bongardt [10] the larvae (no indication of species) are active throughout the year, according to Vogel [129,131] they go into "hibernation," and according to Franz [41] and Newport [95] there is a winter rest period dependent solely on temperature. The larvae of the foreign (specifically American) lampyridae likewise have an inactive winter phase, often in a burrow they make for themselves in the ground (Hess [58] and others). -- As to the diurnal rhythm of activity there are no conflicting observations in the literature; the larvae have only been found at night by their glow.

According to Hess the brilliance of the luminescence is also directly proportional to the activity; according to Newport nutrition, motion, and heat are "light-generating" factors. Thorough investigations are lacking in all cases.

According to Weber [134], periods in the life of the insects may be determined not only by periodic variations in the complex of external factors, but also by endogenous rhythms of the most varied nature, or may depend on both exogenous and endogenous factors. The diurnal and annual activity and luminescence rhythm of the larvae of the two species thus needed to be studied along this line, but also the relationships between periods of activity and periods of luminescence.

The first larvae are to be found in the open regularly between the middle of March and April. This time of appearance is widely variable interbiennially (e.g. earlier in the plains of the lower Rhine than in the Rhenish forest), and is marked by the declining frequency of night frosts. Without regard to natural environmental influences (rainy phase of the moon, etc.), the larvae that do not develop into imagines are active from that time on throughout the summer and fall, as long as the temperature near the ground does not get too close to freezing. At average daily temperatures of about +5° C the larvae become inactive (about the end of November). The behavior of the two species during the winter rest period is different. Phausis makes itself a hibernation hole, constructed in the same way as the pupal chamber. It stays in that hole during the winter months without taking nourishment, either in the normal walking position or curled up on its side. The Lampyris larva spends the winter rest period in its normal daytime hiding place (under stones, leaves, moss, and the like), curled up on its side. Metabolism, development, activity, and readiness to react are reduced to a minimum during this latent period in both species of larvae, but they glow at the slightest vibratory or tactile stimuli. If the temperature of a winter night rises to about 5° C, not infrequently Lampyris larvae may be found glowing and fully active outdoors, but no Phausis larvae.

In the attempt to force the development even during the winter months at room temperature and the usual growing conditions the following observation was made: In both species the desire for food almost completely died out by December; the Phausis larvae in some cases made holes and all became motionless, the Lampyris larvae became sluggish, many of them inactive, but in contrast to Phausis occasionally took nourishment. In this way they spent the winter months (December, January, February). I had considerable losses during that time. -- Parts of the Lampyris broods that were kept through the winter months or for at least 14 days in the refrigerator at -3 to +5° C not only survived the winter better, but when brought into room temperature were normally active after a few minutes and took a moderate amount of nourishment, but went back into hibernation in the refrigerator. This change of activity could be repeated often in Lampyris, but not at all in Phausis. During the winter inactive period in refrigerator larvae I occasionally observed elimination of water through the anus, presumably to raise the resistance to cold (Fig. 35).

The activity of the larvae is thus subject to an annual cycle in which an active phase (seeking and taking nourishment,

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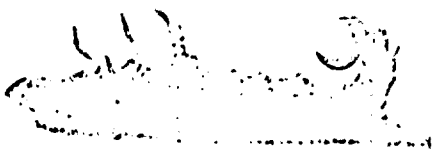


Figure 35. Elimination of water, presumably to raise the resistance to cold (Lampyris larva).

moltings) is followed by a winter rest period. This diapause is total and obligatory in Phausis. Lampyris seems to belong to the mixed reaction type, in which the inner rhythm can be modified by climatic factors, for while the rest period is apparently endogenously fixed, its duration is exogenously variable (partial, facultative diapause), but is not simple numbness from the cold. (Cf. the behavior in the temperature gradient.)

b) Day-and-Night Periodicity of Activity and Luminescence

The diurnal dynamics of insects is by no means always set in motion by the rhythmic variation of light, temperature, and atmospheric humidity, but is also controlled by endogenous components (Weber [134]). Let us consider the relation of endogenous and exogenous influences to activity and luminous capacity.

Outdoors the larvae of the two species are as a rule found only at night, when they glow. Only on dark, overcast days have I found Lampyris larvae (not Phausis!) in the morning or evening hours. Normally they seem to be inactive in the daytime, for even in densely populated habitats search for them is fruitless. The activity of the larvae also appears to be extensively adapted to the seasonally changing length of day and night; i.e. the larvae always appear at the coming of darkness and disappear at the beginning of day, and this means a lengthening of activity in the spring and fall by about six hours.

Because of the difficulty of observing the diurnal variation in activity accurately outdoors, experiments with an actograph were set up.

This consisted of a smoked-paper drum driven by a twelve-hour clock and in contact with a stylus fastened to the end of a balance beam. To the balance beam was attached a light plastic tube in which filter-paper inserts ensured a uniformly high humidity (95-100%). The dimensions of the tube were for Lampyris 45 cm in length, 2 cm in diameter, for Phausis 30 cm in length and 1 cm in diameter. The diameter of the tube was not much greater than the

[illegible] of the larvae. [illegible] direction as long [illegible] after it ready out. In the [illegible] placed only one [illegible], taken from their cultures. [illegible] individuals [illegible] was repeated at least twenty times with the same [illegible] animals. The tube contained no special hiding-place for the larvae, as they could move freely about [illegible] tube. The actograms [illegible] only when they moved from one end of the [illegible] to the other (about 4 cm. [illegible] from the pivot of the balance beam). The experimental temperature [illegible] 3 (p.16). Not only the humidity but also the temperature and lighting conditions were kept constant.

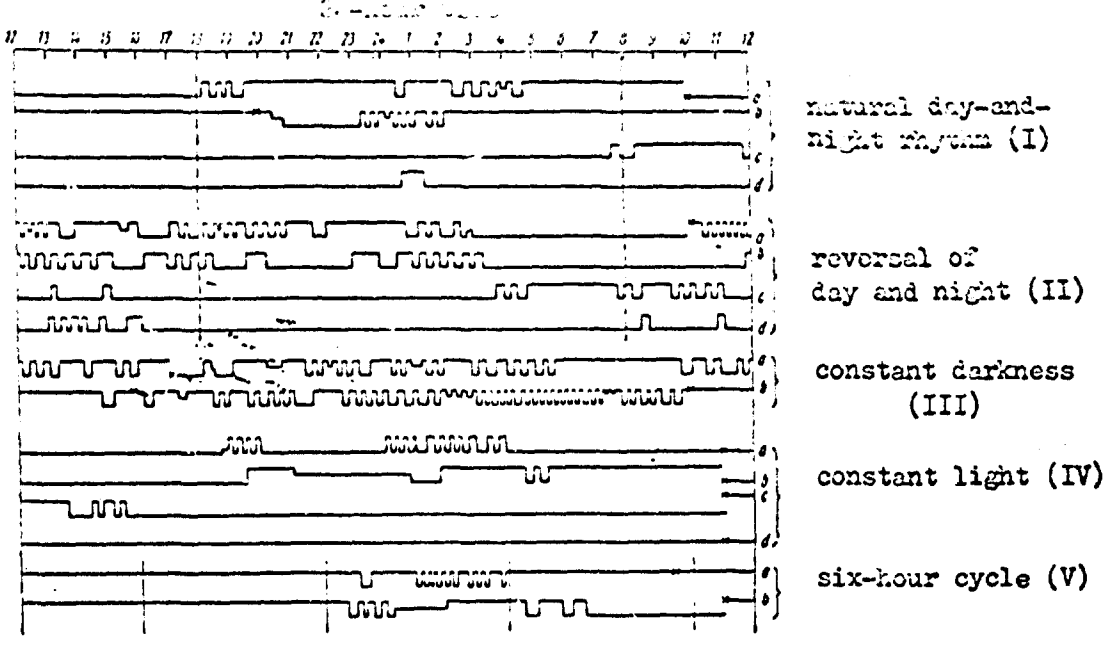


Fig. 36a. Actograms of [illegible] larvae.

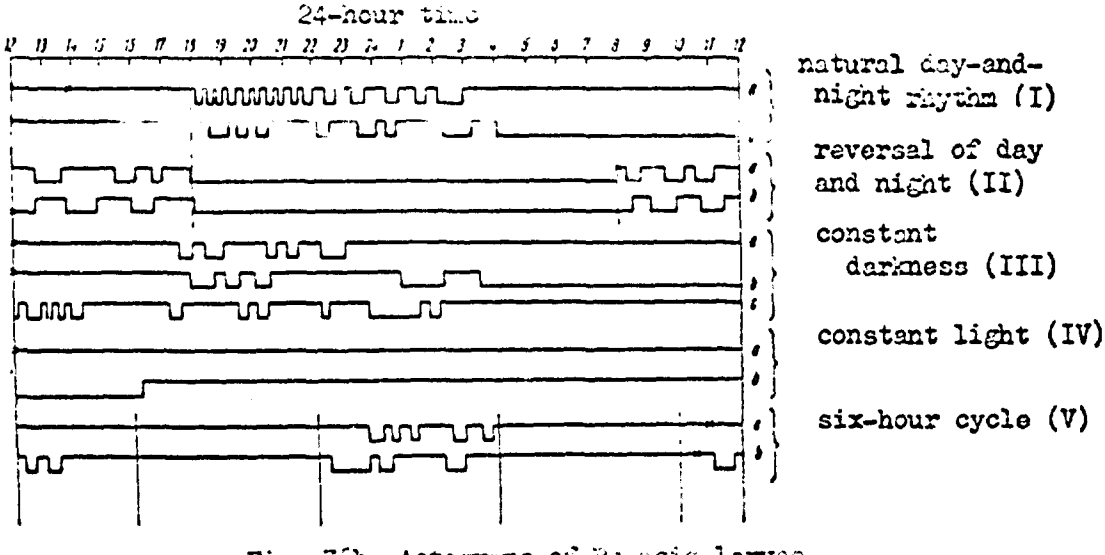


Fig. 36b. Actograms of [illegible] larvae.

The series of experiments gave the following results:

1. Normal day-and-night rhythm (day from 8:00 to 18:00 at 500 lx illumination for Lampyris and 300 lx for Phausis). [See note.]

[Note] The illumination of the experimental space on bright days ran about 500 lx. At that brightness Phausis reacted scototactically, but was indifferent to a diffuse daylight of 300 lx.

Limitation of activity to the night hours; inactive in the daytime (Figure 36a,b [I] and 8-13). Figure 36a (I) c-d shows actograms of larvae sated with food.

2. Day-night reversal (day 18:00 to 8:00, illumination as above). Lampyris maintains the active rhythm for several days, but is also active at "night" (Figure 36a [II], a-b); the normal cycle is gradually broken down and adapts itself to the experimentally provided day-night conditions (Figure 36a [II], c-d). -- Phausis immediately reacts as in 1. above, giving up the natural cycle (Figure 36b [II]).

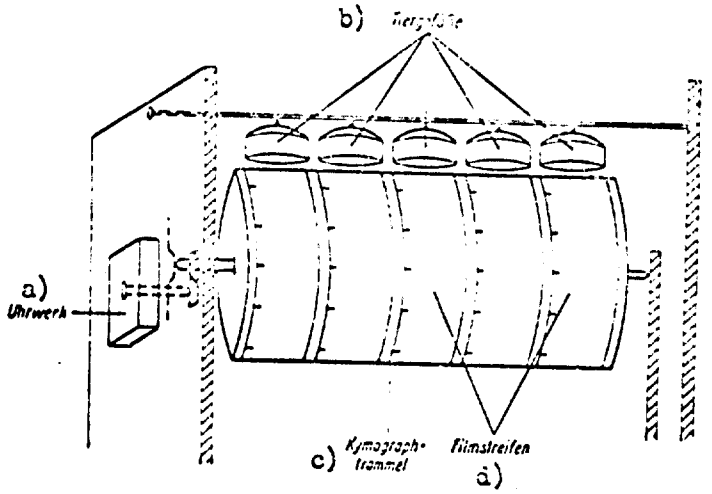
3. Constant darkness. Lampyris is active day and night, with a maximum in the night hours (Figure 36a [III]; Phausis maintains the natural activity cycle (Figure 36b [III], a,b), but with preceding 24-hour constant light the activity begins immediately after darkening (Figure 36b [III], c).

4. Constant light (lighting for Lampyris 500 lx, for Phausis 300 lx). Lampyris: normal day-and-night rhythm is gradually given up, after which inactive or only minimally active (Figure 36a [IV], a-d). With subsequent normal day-night conditions the normal rhythm does not set in again until after several days. -- Phausis: the activity is immediately greatly reduced or ceases entirely (Figure 36b [IV]).

5. Six-hour cycle, light intensity as above. The cycle was so arranged that one period of darkness would fall in the normal daylight hours and one period of light in the normal night hours, so that the short periods completely cut up the normal diurnal cycle (Figure 36a,b [V]). Lampyris shifts the period of activity into the nightly dark hours, extending it occasionally for 2 to 2.5 hours into the subsequent period of light (Figure 36a [V]). -- Phausis is only active during the periods of darkness, and occasionally only during the one that falls during the natural night (Figure 36b [V]). Since the factors of temperature and humidity were constant and only the lighting conditions changed, the results are to be attributed solely to the effect of the light factor. In Lampyris the endogenous component obviously predominates at first, and the endogenous rhythm only gradually adapts itself to the exogen-

[illegible] change in the factors, while [illegible] adjusts itself immediately and exactly to the changed [illegible]. If there is no such alternation in light-dark (constant darkness, constant light), Lampyris reacts in constant darkness as under normal light-dark conditions, -- proof of the fact that an endogenous activity rhythm is not lacking. Photo-stimulation causes Lampyris to exhibit movement (cf. the flashing in the luminescence method). -- All external vital phenomena (capture of prey, [illegible] of nourishment, molting) are restricted to the active phases.

In order to study the luminescence phenomenon of the larvae in connection with the rhythm of activity, the following photokymograph was designed (Figure 37).



a) clockwork

b) vessels containing the larvae

c) kymograph drum

d) film strips

Figure 37. Photokymograph to record the diurnal rhythm of luminescence in Lampyris and Phausis larvae. Explanations in the text.

A drum driven by a twelve-hour clock was covered with highly sensitive film with time marks (Ilford HPS 27/10° DIN). A few millimeters above the horizontally placed drum the vessels containing the experimental animals were suspended. The bottom of the vessels, which was turned toward the drum, consisted of finely perforated, transparent paper; the cylindrical walls were lined with moistened layers of filter paper, which provided for high, uniform humidity. The cover of the vessels was made up of a concave silvered mirror whose focal point coincided with the surface of the film and which reflected all the light from the larvae upon the film. The experiments were carried out at 20° C and of necessity in constant darkness. In each vessel was one larva, which after 24 hours was taken out and not used again. In the vessels there was no place for the larvae to crawl away and hide. The series of experiments were repeated with at least fifteen individual larvae.

The results (Figure 38a,b) show a well-marked rhythm of luminescence for both species. In Phausis it is more precisely limited to [illegible] hours than in Lampyris, and thus corresponds [illegible] to the activity circumstances in constant darkness (cf. Figure 36b (III), a,b). Lampyris larvae, which are constantly active in constant darkness (cf. Figure 36a (III), a,b), nevertheless luminesce predominantly during the nocturnal activity maximum. In contrast to the periodicity of activity the rhythm of luminescence in Lampyris seems to be more strongly endogenously conditioned. -- The darkened places on the film show that the luminescence of the larvae was of irregular intensity and by no means continuous.

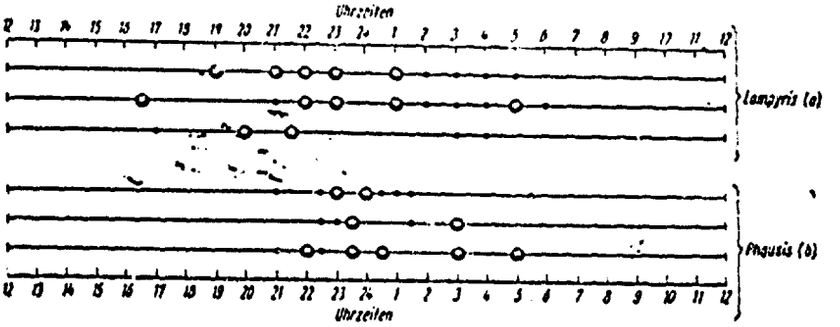


Figure 38. Rhythm of luminescence of Lampyris and Phausis larvae. The different-sized markings indicate glow of varying duration (or varying intensity). Scale: 24-hour time.

2. Alimentation

Concerning the alimentation of the larvae there are conflicting observations and assertions. The majority of the authors report shelled snails as the chief food in captivity (for foreign lampyridae larvae, too) (Fabre, Haddon, Hess, Höllrigl, Hutson, Knauer, Main, Maille, Meissner, Newport, Vogel). According to Hess, Knauer, Main, and Meissner they also eat shellless snails; Newport denies this. They are also said to take vegetable food (Haupt, Knauer, Olivier, Weitlaner). The American lampyrid Pyropyga fenestralis, according to Hess, eats not only snails but also worms and small insect larvae with white cuticula (Leptinotarsa decemlineata Say, Paragrotis species, Peridroma margaritosa Haworth, Anosa tristis De Geer).

Attacks on snails have been described for Lampyris by Fabre, Haddon, Hess, Hutson, Maille, Newport, and Vogel [129]. Since these observations were made under the most varied conditions in captivity, they are incomplete and partially contradictory (probably because they were not repeated or not

reported [illegible]). How the larvae find and [illegible] the snails is not reported, or chance is assumed (Haddon, [illegible]); [illegible] are lacking. I have found no statements concerning the predatory activity of Phausis.

Following [illegible] observations of [illegible], Faure and especially Vogel's thorough morphological studies [127 129], the larvae of the Lampyridae have since passed for carnivorous, extraintestinally digesting, specializing on snails as food, and first paralyzing the snails with the extraintestinally digesting secretion of the intestine. (Haddon denies this last.) I shall deal with the findings of these authors later in detail.

c) Prey

In the open I found both species feeding only on shell-less and shelled snails (species of Limax, Cepaea, Succinea, Vitrina, Monacha, Eulota, and Clausilia), and Lampyris in one case on a crushed blindworm (Anguis fragilis). In captivity they took almost any shelled land snails and shell-less snails offered to them, as long as they did not exceed a certain size (shelled snails for Phausis not larger than about 10 mm in diameter or height, for Lampyris up to the size of full-grown Cepaea; shell-less snails could be up to about twice as long as the Phausis or Lampyris larvae). Besides the above-mentioned species they ate Zebrina detrita and obscura, Helicella ericetorum, striata, and candidans, Helix pomatia, Arianta arbustorum, Isognostoma personatum, Fruticicola hispida, Oxychilus cellarius, Vitrea crystallina, and Arion species (A. empiricorum, A. subfuscus, A. hortensis, A. circumscriptus). But many land snails with tough, hard, or dark flesh they took only when hungry or scorned them entirely (e.g. Limax maximus, L. cinereoniger, Arion species, Oxychilus cellarius pieces of old specimens of Helix, and the like). From the enumeration it will be seen that the larvae even eat xerophilous snails that occur in their biotopes rarely or not at all (Helicella, Zebrina); they very avidly eat water snails (Lymnaea stagnalis and auricularia, Planorbis corneus). In captivity they also take earthworms, frog meat and mammalian meat (lean beef), mashed, dead larvae and mashed females of their own species; living or dead undamaged specimens of their own species are not attacked or devoured. Systematic feeding experiments presumably could reveal a still more extensive list of foods. In particular it is to be assumed that they attack animals of ground habitat and soft slimy consistency and that even in the outdoors they feed on animal cadavers that offer access through wounds to soft body parts. Older, slightly putrescent cadavers (including those of snails) they leave untouched. Living caterpillars and maggots of various ground species were not accepted. In tests of choice the larvae always preferred snails as food. This fact and the biological and morphological adaptations permit the conclusion that snails constitute the

principal food.

The quantity of nourishment is widely varied and is of course determined by the size of the larvae. They attack snails up to 15 times their own weight and devour them completely as a rule within 24 to 36 hours (at room temperature). If a snail has freshly taken on plant nourishment, they leave parts of the snail's intestinal tract untouched (evidence tending against a phytophagous habit of alimentation!). The larvae take food until their intersegmental membranes are stretched to the maximum; in this way they can expand to almost double in length and width and quadruple their body weight. A larva that has eaten its fill in this way spends several days motionless in its hiding-place (cf. Figures 36a [2], c-d). Both species can also go without food for months at a time, however. (At room temperature, after five months over half the subjects were still alive.)

The water requirements of the larvae are generally covered by the diet of snails. If intake of food is prevented (for only about four weeks at 95 to 100% relative humidity!) the larvae eagerly drink water, which they can also absorb when it is held in a capillary state (e.g. from moist sandy soil or filter paper).

Water taken in in too great abundance via the snail diet is eliminated during or soon after the intake of food as a thinly liquid urine, clear as water, which leaves crystals behind after drying out (uric acid?). This quick excretion of water is to be observed especially during and after big meals, and of course makes it possible for the larvae to take in more food. In addition the elimination of water may improve the greatly impaired mobility of the bloated larvae. It is interesting that urine is also secreted in cleaning [the mouth parts] after a meal to soften the occasionally already dried snail slime (see below). The rest of the food does not finish passing through the intestine until a day or two later, and the indigestible remnant is excreted in the form of more or less liquid feces. This is of a greenish color and smells like a smashed snail. A mature larva that has eaten its fill excretes about 0.05 to 0.2 cm^3 of feces after

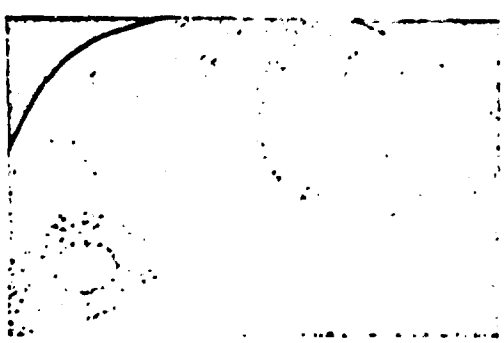


Figure 39. Marking left by feces (evidence against extraintestinal digestion).

several cm. thick on filter paper leave zones marked by different colorings (Figure 39; evidence against extra-intestinal digestion).

b) [illegible]

After detailed earlier observations I fixed myself, for more exact analysis of the predatory activity, a terrarium 1 x 1 meter in size, in which the ecological conditions were carefully taken into account. I made my observations only during the nocturnal periods of activity of the larvae, by red light (not over 20 lx; cf. page 26). The prey used consisted of shelled and shell-less snails (mostly various species of Succinea and Limax agrestis respectively).

a) Normal sequence of prey. -- Capture of prey by both species runs the following course: Constantly checking the surface of the ground with movements of the feelers and antennae, the larvae follow the snail. When the snail is reached, it is eagerly felt over. Maintaining constant feeler contact, the larvae then search -- usually crawling along one side of the snail --for the fore end.

Not until the fore end is reached (i.e. in the case of shelled snails and Arion species about the foremost quarter, in Limax species the fore part up to the shell) do they begin the attack. Usually opening the mandibles repeatedly, they feel so cautiously and softly over the fore end of the snail that it usually does not even pull in its feelers. Then with maximum extension of the head they make a powerful, rapid bite, usually in the vicinity of the feelers, after which the larvae immediately back away and retract the head (defense posture). Shell-less snails retract feelers and head as far as possible and strike out violently with the tail, with coiling motions of the whole body. Shelled snails retire as fast as possible into the shell. During these defensive movements both secrete a more or less great amount of slime, but do not fall from their support.

In what follows it is largely the further behavior of the Lampyris larva that is described. It behaves in a way that differs typically depending on whether the larva has attacked a shell-less or a shelled snail. In the case of shelled snails it very soon gives up the above-described defensive attitude, goes around the retracted snail once or more, always feeling, and finally climbs up on the shell, takes a position facing the opening of the shell, and holds fast with the pygopodium. In this position it keeps the opening of the shell under observation by feeling (Figure 40). Often the snail closes the opening with a thin mucous membrane and may

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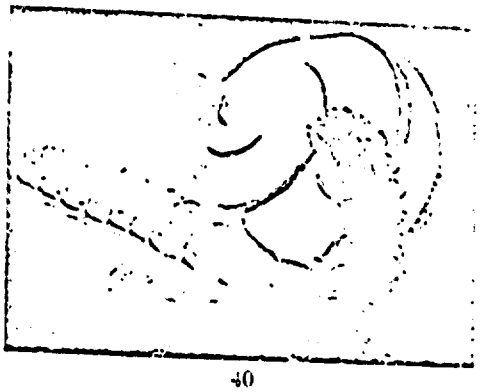

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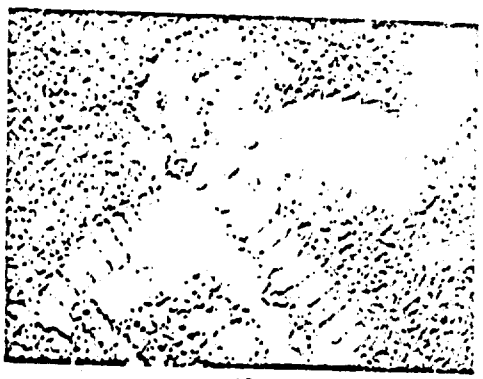

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Fig. 40. [illegible] larvae attack a snail (Limnaea): lying in wait, observation of the opening.

Fig. 41. Lampyris larva rides on a shelled snail (Cepaea): bite in the fore end of the fleeing snail.

Fig 42. Attack of several Lampyris larvae on a shell-less snail (Limax): bite always into the fore end, even when the rear end comes very close to the fore end.

remain thus, inaccessible to the larva, for hours. It does not force its way into a shell closed with a mucous membrane or epiphragma. During this time the larva leaves its prey, if at all, only for a moment to make another circuit around the snail or to clean itself (see below). A hungry larva returns again and again to the snail shell and continues to check its opening. I have seen larvae persist in this concentrated lurking position for more than twelve hours. -- As a rule, however, the snail tries after a short time to run away with its dangerous rider. But, thanks to its constant observation, the larva perceives every movement of the snail, and as soon as the latter comes out of its shell, thrusts its head or -- depending on the size of the snail -- its whole body far forward in order to bite into the snail's feelers or close behind them (Figure 41). The snail retracts repeatedly, secreting slime; the larva checks on the shell opening from the shell or from the ground, and depending on the size of the larva relative to the snail this may be often repeated, until the snail is paralyzed, often after many hours. Finally the snail is no longer capable of closing its shell opening with slime, or it can no longer hold fast to its support,

[illegible] shell edge over, or the snail is no longer able to retire completely into its shell.

[illegible] the [illegible] shell-less snail as a rule its locomotor movements are greatly impaired after the first bite. After keeping a short while in the defensive posture mentioned, the larva follows the fleeing snail, overtakes it, and again bites into the head end. Usually after this the snail is no longer capable of locomotion; in any case bites into the fore end of the snail are repeated in rapid succession until the snail is completely motionless. Shell-less snails are never climbed upon during the attack (Figure 42).

After careful feeling over the whole snail and a further series of bites, to which the snail no longer reacts, the paralized shell-less or shelled snail is seized and carried away in a measuring-worm-like backward motion. During the transport the larva often leaves the snail to undertake excursions in the neighborhood. These excursions run more or less concentrically with the prey as the center. Upon encountering obstacles that could serve as suitable hiding places the larva makes striking searching movements (decelerated speed of locomotion, slow vertical and horizontal movements of the fore part of the body), and crawls under the obstacle, to reappear only after a considerable time. But these excursions always lead back to the prey. Each time it is felt around from all sides and dragged farther. The transport ends in a hiding-place, often after a distance of meters. This behavior of the Lampyris larvae is often wanting in well protected habitats and also often in the case of larvae that have been without food for several months.

The attacks of Phausis larvae on shelled or shell-less snails are less differentiated. Both kinds of snails are attacked and paralyzed in about the way that Lampyris attacks shell-less snails. But the shell opening of shelled snails is just as persistently and carefully watched. Only rarely do Phausis larvae climb up on the shell. The Phausis larva usually leaves the paralyzed snail right where it is and immediately begins with its meal. Occasionally, however, I was able to observe it, too, dragging its prey away.

Cleaning up (Figure 43) is a conspicuous activity. In the case of Lampyris it is accomplished almost solely with the pygopodium, which is also useful in locomotion and in molting, and which consists of many separate whitish tubes which can be thrust out from the anus by bloodpressure and drawn back in by musculature. The Lampyris larvae are so mobile that they can clean all parts of their body. The pygopodium "grasps" the adhering particles of slime and dirt, pulls

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Fig. 43. Cleaning the mouth parts with the pygopodium after an attack on a snail.

[illegible] wipes them off on the ground with a characteristic abdominal motion that occasionally is repeated several times. [illegible] the larva often [illegible] already mentioned. During the attack, the [illegible], and the [illegible] cleans itself [illegible], but after the meal is over it cleans not only its head and mouth parts, but the whole body and legs, very carefully. The cleaning movements of the pygopodium can also be induced experimentally with sticky substances of all kinds (paste, exsiccator grease, etc.), and by sprinkling with bits of dirt. In the cleaning and in the transport of the prey the great adhesive effect of the anal tubes is evident. The retractable tubes work like vacuum cleaners. The effective cleansing from the very sticky snail slime is thus accomplished not only by these movements of the pygopodium, but simultaneously by a suctional and adhesive effect of the pygopodium. In addition the larvae occasionally brush themselves off with their legs.

In the Phausis larva cleaning with the pygopodium is rarely observed, and because of the clumsiness of the larva is probably also less successful, for often for days after the attack the larva is still covered with slime on spots that are hard to reach (e.g. tergites). In Phausis the usual cleaning with the legs predominates.

b) Experimental analysis of the behavior and its psychological components. There had previously been no experiments concerning the larva's capture of prey. But by mere observation alone various parts of the series of reactions cannot be explained, such e.g. as the way of finding and following the snail (I), the finding of the fore end of the snail (II), the differing behavior in attacking shell-less and shelled snails ("riding") (III), the causes for dragging away the snail and for the excursions that take place in connection with that (IV), and the effects of interventions in the normal course of the predatory behavior pattern (V).

The following experiments were done with Lampyris (I, 1,2,4; II, 5a,b with Phausis as well):

I. Discovery and Pursuit of the Snail

While Fabre, Hutson, Maille, and Newport [illegible] statements on this question, according to Haddon and [illegible]

is found by chance, and according to Vogel by scent and sight.

1. Sense of smell as perception at a distance

a) Snails crawling into the immediate vicinity of hungry larvae are not perceived.

b) Test in the Y-tube with air current. A Y-shaped tube (diameter 1.5 cm) [illegible] the short leg (11, 11, and 6 cm) was attached [illegible] to a water jet pump (velocity of the air current [illegible] cm/sec). Filter-paper [illegible] humidity of the system. The larvae were introduced at the end of the short leg; at the end of one of the equal legs was a living snail (shell-less or shelled), in the other a filler of equal size, so as to keep the flow conditions in the two legs equal. The snail and the filler were often exchanged.

The result (Figure 44a,b I) is negative, as it hardly deviates from a ratio of 1:1.

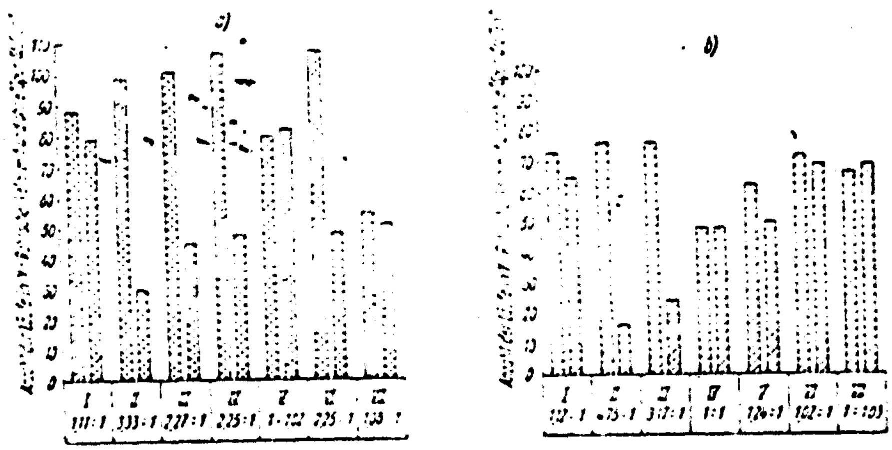


Figure 44. Discovery and pursuit of prey: a) Lampyris larvae, b) Phausis larvae. I: air current system, II: slime of shelled snails, III: slime of shell-less snails, IV: earthworm slime, V: human saliva, VI: exsiccator grease (stopcock grease, Merck), VII: control, distilled water. Left: values for the leg with the "spoor material," right: values for the leg without the "spoor material." Vertical scale: number of runs made in the Y-tube with and without "spoor material."

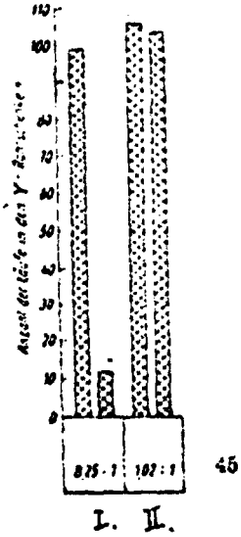
2. Following the snail slime spoor

a) In observation of the predatory behavior it is noticeable that the larvae set on a trail of snail slime follow the trail exactly, even if it leads over obstacles of all kinds (ground flora). In the same way the larvae follow snail

slime trails artificially laid (even if they are drawn in many windings).

b) For further testing, Y-tubes were again used (diameter 1.2 cm, length of legs 10, 15, 20 cm). To eliminate klinotactic reactions, the bottom of the tubes was [illegible] uniformly moistened (with distilled water), filter paper, on which a trail of snail slime led from the [illegible] one of the long ones. The hungry larvae are introduced [illegible] short shank. The results (Figure 44a,b I-III) are positive for both species on the slime of shelled and shell-less snails. It is interesting that Lampyris also follows trails of earthworm slime and exsiccator grease (Figure 44a IV and V). Phausis pays no attention to trails of substances with a sticky or slimy consistency (Figure 44b IV-VI). Compare with this the control experiment (Figure 44a,b VII) without slime trail on moistened filter paper.

3. Amputations of the feelers of antennae and maxillae (performed only on Lampyris). According to Vogel's morphological studies [128] the organs of touch and smell are on the antennae and feelers. Amputation of one or both organs to the base should therefore result in corresponding loss of those senses. The amputation was performed under CO_2 narcosis. Four days after the amputation the hungry larvae were put into the Y-tube described under 2b). This yielded the results shown in Figure 45.



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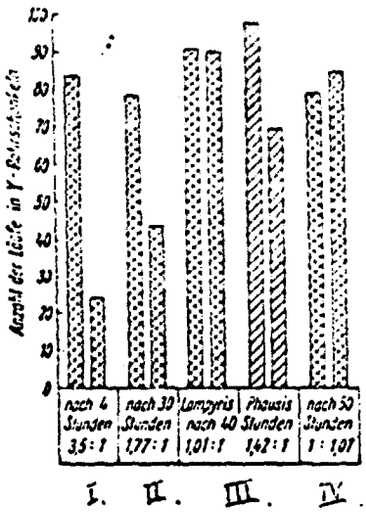

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Vertical scale for both figures: number of runs in the two shanks of the Y-tube.
Legend for Figure 47:
I: after 4 hours
II: after 30 hours
III: after 40 hours
IV: after 50 hours

Right: tube without slime trail

Lampyris Phausis

Figure 45. Following of the trail of snail slime: Lampyris larvae I with antennae amputated, II with maxillary feelers amputated. Left: values for the leg of the apparatus containing the slime trail.
Figure 47. Duration of effectiveness of the trail of snail slime.

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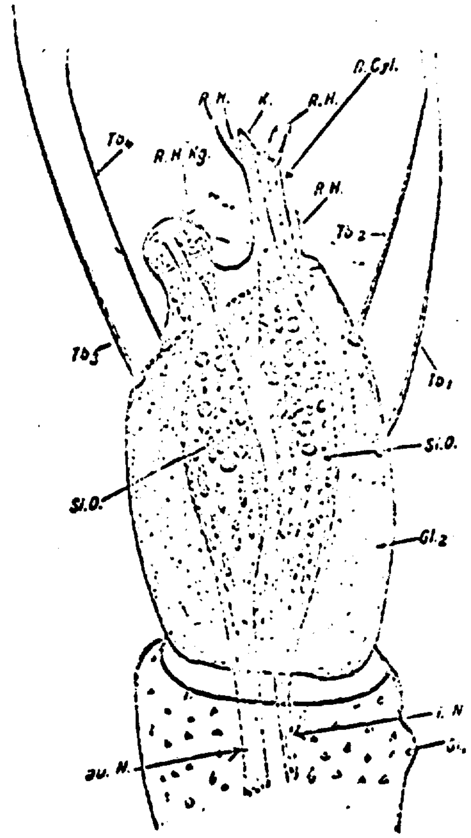

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[illegible] of the anten- [illegible] (according to [illegible]). The second or terminal joint [illegible] with the two [illegible]," the olfactory cylinder [illegible]. Drawn from a [illegible] larva.

[illegible] - [illegible] branch of the antennal nerve

Gl. 1,2 - joints of the antenna

[illegible] - [illegible] branch of the antennal nerve

K. - cone

R.Cyl. - olfactory cylinder

R.H. - olfactory hair

R.H.Kg. - olfactory bulb

Si.O. - sense organ

Tb. 1-4 - the four big feeler bristles of the terminal joint

Zeiss ocular 3, objective C.
Zeiss apparatus.

The ability to perceive and follow a snail thus appears to belong solely to the feelers, in which we must therefore look for the corresponding receptors. Antennaless animals with feelers behave quite normally in these experiments, while feelerless ones with antennae do not follow the slime trail, so that it must be assumed that the antennae have no function in the capture of prey. Vogel's explanations of the sense organs of the antennae would have to be revised (see Figure 46, R.Hkg, R.Cyl., R.H.). On the lobus externus of the first maxilla and on the labial feelers it is obvious that no special sensory cells are localised that make it possible to pick up and follow the trail of snail slime. The rest of the predatory behavior of the larvae with amputations was normal; those with no feelers, however, had to be brought into direct contact with the snail each time.

4. Duration of effectiveness of the trail of snail slime. Y-tube experimental arrangement as described in 2b). According to Figure 47 [page 68] Lampyris larvae can follow a snail for 1 1/2 days, Phausis larvae somewhat longer yet. For Phausis

a test was made only after 48 hours. Lampyris larvae did not react to such trails.

2. Finding the fore end of the snail

This problem is of interest among other reasons because the fore end of the snail contains the cerebral and pedal ganglia, through which paralysis of the snail may be produced more quickly (cf. Chapter C III, 2c δ).

Vogel [128, page 369] assumes on the basis of the structure of the eye and the precisely executed bites that the larvae can see not only their prey as a whole, but also its tentacles. That the larvae as a rule go in search of food at night tells against this assumption. Since the results of 1. do not exclude a simultaneous optical perception, the following experiments were carried out:

1. Blind, hungry larvae (eyes covered with a coating of lampblack and shellac) were set on a trail of snail slime.

The result corresponded to the observations presented in Chapter C III 2b. The predatory behavior (finding the snail, finding the fore end of the snail, attack, climbing on the shell if any, keeping the fore end under observation, dragging the snail away, and taking food) took the same course as in "sighted" larvae.

2. Amputation of feelers and of head of snail:

a) Both pair of feelers of the snail (shell-less or shelled) were cut off in succession, but the fore end was still found in the attack (Figure 48).

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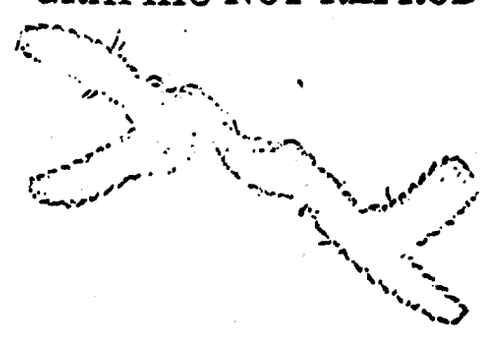

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Figure 48. Finding the fore end of the shelled snail when the snail's pairs of feelers have been amputated.
Figure 49. Finding the fore end of the shell-less sn 1: Lampyris larvae on a combination (fore end of a snail on the rear end of another snail).

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50 51

Figure 50. Finding the fore end of the shell-less snail: combination of rear end of snail + fore end of another snail.
Figure 51. Finding the fore end of the shell-less snail: combination of fore end imitated in elderberry pith + rear end of snail; piece of elderberry pith smeared with slime from fore end of snail.

b) The head was cut off. (This could be done only in the case of shell-less snails, as shelled snails withdraw into the shell and do not come back out.) The results were the same as in 2a).

3. Combinations of snail bodies:

a) To the rear end of a shell-less snail was sewn the fore end (= part up to the rudimentary shell) of another, which the snail dragged along behind it. Both ends were bitten (Figure 49).

b) The head of a shell-less snail was attached to the rear end (= part behind the rudimentary shell) of another. Bites occur not at the ends (tips of tails), but at the head part in the center of the snail combination (Figure 50).

4. Half dummies:

a) The fore end of a shell-less snail was combined with a piece of elderberry pith imitating the rear end and smeared with slime from the fore end. (The pith of the elder bush was used for this and the following dummies because it is lighter than plasticine and the like, did not give way at the joint with the snail, but still could be carried by the injured snail. Also, it is odorless and tasteless, and snail slime sticks better on it.) Reaction as in 3a).

b) An elderberry pith fore end with fore-end slime on a snail rear end: reaction as in attack on a normal shell-less snail -- bites in the artificial fore end (Figure 51).

c) An elderberry pith rear end smeared with rear-end slime on a real snail fore end got no bites. The larvae felt

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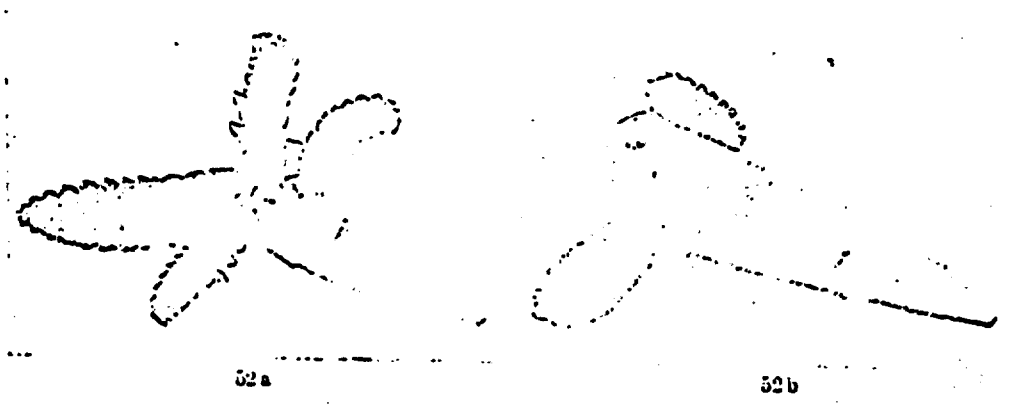

52a 52b

Figure 52. Behavior toward the elderberry pith dummy [(a) Lymnaea, (b) Phausis]: to the left of the dark line slime from the fore end of a snail, to the right (pointed end) slime from the rear end.

along it to the fore end.

d) Slime-free bits of elderberry pith at the fore end of the snail were disregarded.

5. Complete dummies:

a) In accordance with what was learned from II 3-4, an elderberry pith dummy crudely imitating a shell-less snail was smeared at one end (blunt end) with fore-end slime, at the pointed end with rear-end slime. The larvae bit into the blunt end (Figure 52a) and even dragged this dummy away.

b) Since the above experiments (II 2b-4c) could be performed only with shell-less snails (see the note under 2b), the same dummy was tested with corresponding distribution of slime from shelled snails, and with the same result.

Since Phausis larvae react to small interferences with long-lasting akinesis, only experiments 5a and 5b of series II were done with them. This check, however, confirmed for Phausis the same capacity for distinguishing fore end and rear end of the snail by the consistency of the slime (Figure 52b).

III. Climbing on the Shell and Riding

1. Over the mantle of a shell-less snail an empty snail shell is mounted. After the first bite the larva climbs on the snail shell only in those cases when the snail (or at least its fore end) entirely disappears under the shell in the ensuing lengthwise contraction.

2. Conically pointed paper shells or flat-fitting bits of paper are climbed upon like the shells of shell-bearing

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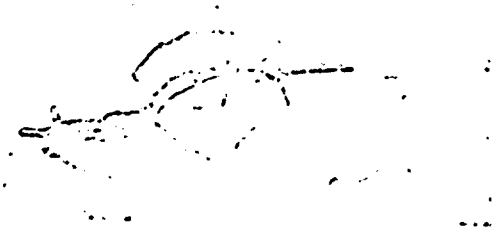

Figure 53. Climbing on a paper "shell" [illegible]

shells, if large enough and pulled down at the start (figure 53). Under both conditions (1 and 2) the larva "rises" upon the fleeing shell and continues its attack from that vantage point. In these cases the larva always orients itself toward the fore end of the shell.

3. Shells or bits of paper that are too small either are not climbed upon at all or the larva merely holds on there with its legs, while fixing itself to the ground with the pygopodium.

With shell-less snails there is a different situation in that after the defensive movements induced by the first bite they immediately attempt to flee, and the larvae respond to this immediately with pursuit or another bite. If the body of the snail is covered after the first bite on the side toward the larva, the larva will immediately climb up on the cover.

4. A cover smeared heavily with slime (shell, paper, and the like) is rarely climbed upon.

IV. Seeking a Hiding-Place for Feeding

1a) Nearly flat terrain without cover (sandy soil).

The larvae often run about for hours with their dead or paralyzed prey, leave the prey to search about for long periods, and all in all cover several meters' distance before they finally begin to feed.

b) Dense turf.

The larva either does not drag its prey at all or only drags it a short distance into the thickest growth. It very soon begins to feed.

2a) The larvae of 1a) immediately accept leaves, moss, bits of paper, and the like as a hiding place and begin to feed.

b) If a possible hiding place is put in the way of a larva that has for the moment left its transported prey and is

moving about with typical searching movements, it crawls under, stays there for a fairly long time, reappears, again disappears under the shelter, etc., until finally it goes back to the prey, as a rule takes the prey to the hiding-place, if the distance between prey and hiding-place is not greater than 5 to 10 cm. In other cases it often misses the so carefully "investigated" hiding-place (cf. on this point Chapter [illegible], thigmotaxis).

3. Finding the prey after moving away from it.

a) The larva in the course of the concentric excursions normally always comes back to the dragging trail, which is then followed. Coming back into the dragging trail is often signalised by lighting up.

b) If the prey is taken away during the larva's excursion, the latter comes back (in accordance with 3a) to the place where the prey was lying. Then with noticeably irregular searching movements (horizontal and vertical movements of the fore part of the body) it either runs up and down the dragging trail or searches around in a wide circle.

V. Interventions in the Normal Predatory Behavior

1. If the snail is taken away just after it has been overcome, the previously so cautious larva behaves as described under IV 3b).

2. If this larva (or V 1) is presented with a fresh, living snail, it repeats the entire attack, but without being able to overcome it even after hours of pursuit and dozens of bites (see next chapter, 2 c δ).

3. If living snails are brought to a larva that has just overcome its prey, it does not leave its prey and does not attack the new snails, even if they crawl over the head or under the mandibles of the larva. Likewise the larva does not attack living snails during its excursion, but goes back instead to the paralyzed prey.

4. If a hungry larva is put beside an already injured snail or a freshly cut piece of a snail, it begins -- without the actions preceding the capture of prey (pursuit, attack, etc.) -- to drag the prey away or to devour it immediately (depending on the conditions of IV a,b).

5. If hungry larvae meet a larva that is dragging away its prey, they immediately attack it in order to carry the prey away themselves. They pull in all directions or the majority or the strongest larva "takes over" the direction and all the rest, hanging on by their teeth, are dragged along against

their will.

6. Movements artificially established in the prey immediately arouse the attention of the otherwise cautiously waiting ("lurking") larvae, which begin to attack.

The results of observations and experiments show that the capture of prey consists of a series of consecutive, typical actions, which always follow upon a definite key stimulus.

1. Coming upon the trail of snail slime → pursuit.

2. Finding the snail → overcoming up to the fore end (marked by a different type of slime).

3. Palpation of the fore end of the snail → attack (first bite).

4. Defensive reactions of the snail (and/or withdrawal into the shell) → protective and lurking posture of the larva.

5. After an indefinite time (source of stimulation?) → climbing up on the shell in the case of shelled snails.

6. Flight (locomotion) of the snail → repetition of 2 or 3 to 5 until the snail is motionless.

7. Motionlessness of snail (paralysis, death) → dragging away of the prey.

8. Finding of a hiding-place (satisfaction of positive thigmotaxis) → halt of transport, taking of nourishment.

This stimulus-reaction chain is not rigid; various intermediate steps may be readily repeated (V 2) or skipped (V 4,5). The mode of action to be chosen accomodates itself flexibly to the given stimulus-reaction situation between prey and larva.

The chemical senses (smell and taste) and the sense of touch must play the decisive rôle in the predatory behavior. The sense of smell, however, does not operate at a distance. Sight and sense of form play no part.

The capture of prey differs fundamentally from the practices of other snail specialists among the beetles or beetle larvae. In the other cases either the shell is broken open and the snail overcome by pure mechanical force (many carabidae) or the attackers penetrate, regardless of the masses of slime that the snail secretes as it withdraws into the snail after the first bite, through the opening of the shell to the soft body of the snail, which they eat alive (Drilus [see Note] and Sulphidae larvae).

[Note] According to my own observations.

[illegible]

In order to be able to understand the processes during the taking of nourishment, it is necessary to produce a few remarks concerning general and specific morphological and physiological conditions in the larvae (s. also).

α) Morphological adaptations (especially of the mouth parts and the intestinal tract) to the procurement of food.

The cychrization often found in insect enemies of the snails (acumination and elongation of the fore part of the body and of the head, elongation of the mandibles) is not very marked in Phausis and Lampyris. It is limited merely to the formation of a small, narrow head (in a [illegible] 0.9 cm long, 1.35 x 1.1 mm; in a Phausis 0.65 cm long, 0.9 x 0.55 mm); in any case the whole body is flattened and slender (of the above-mentioned lengths, Lampyris up to about 6 mm wide, Phausis up to 4 mm). Lampyris and Phausis larvae exhibit other adaptations to their snail diet. Thus the connective membrane between prothorax and head allows them a long forward reach, and the long membranes connecting the individual parts make possible the telescope-like extension and retraction of the antennae and feelers. Prognathous location of the mouth parts, marked hairiness and bristliness of the whole larva, special arrangements of hairs on the spiracles, and the use of the pygopodium as a cleaning apparatus are other such phenomena.

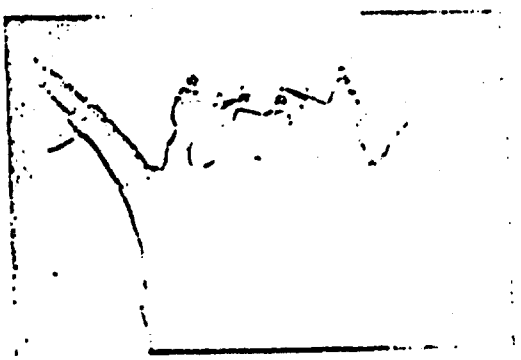

Figure 54. Head and mouth parts of a Lampyris larva. Appendages of the head from outside to inside: antennae, mandibles (and canals), maxillary feeler + external lobe of the first maxilla, labial feeler.

In comparison to their close relatives (cantharidae) the mouth parts are markedly specialized (Figure 54). They show points of similarity to those of the dytiscidae, as may be seen from Haddon's and Vogel's expositions for Lampyris and Höllrigl's for Phausis.

The intestinal tract (Vogel [129]) is not greatly adapted apart from the pharynx and the muscular proventriculus. Only those two segments are suited to serve as pressure or suction pumps.

β) [illegible]

[illegible] the coleoptera as representatives of extraintestinal digestion it is chiefly the [illegible] and [illegible] of the dytiscidae [illegible] of [illegible] and the larvae of [illegible] and [illegible] the larvae of the lampyridae that are mentioned.

According to [illegible] intestinal digestion takes place [illegible] According to Fabre the [illegible] snail is converted after the action over a period of one to two days of an intestinal secretion into a brownish "bouillon" which runs out if the shell is tipped over. According to Vogel a brownish intestinal juice dissolves the snail tissue completely into a thick chyme, in which (after eosin staining) he himself never found cell nuclei or tissue fragments, even in the esophagus ([127], page 519; [128], page 422). The liquefied nutrient broth is supposed to be taken in partly through the mandibular canals, partly through the oral aperture. The diagonally arranged pattern of hair on the lacinia and the bases of the mandibles, pointing forward and toward the median, is conceived of as a sieve apparatus which holds back solid particles of food. On the basis of Vogel's morphological findings, Hess [58] reports largely extraintestinal digestion for the American lampyrid Pyronyma fenestralis, too, but observes that pieces of food are also taken directly into the mouth. Haddon [51] and Newport [95], who also concerned themselves with food intake in Lampyris, make no statements about the actual intake of the food; Haddon does, however, postulate on the basis of the hair arrangement a sieve effect during food intake which would make it possible to take only liquid nourishment.

Fabre, Hess, Newport, and Vogel state that the bites during the attack have a poisonous effect, but Vogel, on the basis of his morphological studies (lack of venom or saliva glands), is the first to suggest connections with the extraintestinal digestion, with the secreted intestinal juice having a simultaneous toxic effect via the ganglia especially on the locomotive organs of the snail. But there are no more precise statements as to the effect of the poison on the snail. The snail is said to be paralyzed first and then die (Newport, Vogel) or to recover after the paralysis (Fabre). Haddon denies any paralyzing effect on the snail from the bite of the larva.

γ) Process of Taking Nourishment in Lampyris and Phausis

Statements concerning the intake of nourishment by Phausis are lacking; for Lampyris they are quite scanty and incomplete (Vogel [129]), because when disturbed the larvae

can retract the head into the prothorax while keeping the mandibles sunk into the flesh of the prey, and so appear to continue eating. With the shelled snails that most authors have fed to their insects the eating process cannot be seen in any case. I observed the food intake mostly on shell-less snails or pieces of snail. But in order to be able to see the eating process in shelled snails, I used snails with delicate shells (Succinea, Lymnaea, young specimens of Cepaea hortensis) which could easily be broken in such a way that the pieces remained in place and could be removed for observation (under 15 to 20-fold binocular magnification).

The process of food intake is the same for both species of larvae and for shelled and shell-less snails. The slime secreted by the snail during the attack is not avoided (Newport), but is taken first, before the larva gets to the flesh of the snail. Chewing involves the mandibles and the bristle-covered, brush-like laciniae. The mechanical chopping of the prey is accomplished (clearly visibly) by the mandibles, which pound away rhythmically for hours and even days (about 60 to 100 times a minute at 15-20° C). In this action the mandibles scissor past each other, each crossing under and over the other alternately. In this way the flesh is quite visibly cut up, and when more or less well chewed and pulverized is immediately pushed into the oral cavity. This moving is accomplished chiefly by the laciniae, whose bristles in the food-intake position are pointed forward and toward the median, in rest position toward the median. The laciniae move laterad, their lateral side then moves upward, and they thus shovel the chewed food from right and left simultaneously toward the oral cavity, moving mediad in the shovel position described. This action of pushing the food in is doubtless effectively furthered by the arrangement of the bristles on the laciniae (see above), for the bristle-covered surface, offering more resistance, is better suited to the transport of slimy bits of food than a smooth chitinous surface. Besides the laciniae the inner mandibular teeth (which are present only in Lampyris) also assist not only in the chopping but also in pushing the particles in. They complement the shovel action of the laciniae. The position of the bases of the mandibles during the chewing motion and the hairs with which they are covered, the hairs of the lower inner edge of the mandibles, and the suction mechanism of the pharynx should assist in conveying the food into the intestinal tract.

The assumption of intake of nourishment through the mandibular canals, such as Fabre and Newport report as the exclusive mode and Haddon, Hess, and Vogel as occurring side by side with the normal intake through the mouth, is opposed by

the mere observation that parts of snails as big as the larva's head are crammed into the oral cavity, that whole snail radulae three times as wide and many times as long as the diameter of the mandibular canal are found in the larva's intestine, and that the tiny openings of the mandibular canals are situated in a place unfavorable for intake of nourishment (in view of the movement of the mandibles the inner side would be more suitable).

During the action of the mandibles the larva, with its mandibles opened (!), secretes every few seconds a watery hyaline liquid, which seems to come not from the mandibular canals but from the oral cavity.

During the one to two-day intake of food the snail is completely devoured, so that only the shell (in the case of shelled snails and species of Limax) is left. Occasionally parts of the intestinal tract are also left, which by their greenish contents suggest that vegetable food has just been taken (evidence against herbivority [of the larvae]). After carefully cleaning itself at the end of the snail meal, the larva, which is often too full to move, spends several days in complete inactivity (cf. actogram, Figure 36a (I), c-d).

δ) Experiments Bearing on the Question of Extraintestinal Digestion and on the Poison Effect on the Prey

I. On the Question of Extraintestinal Digestion

The immediate intake of the chopped food made possible the following checks on both species of larvae:

1. The heads of larvae that had just eaten their fill were cut off and the bits of food found in the oral cavity examined histologically. Result: The cells of the snail flesh showed no signs of digestion and were almost all still in the tissue arrangement.

2. After hungry larvae had been uninterruptedly feeding for 50 hours (so that the entire intestinal tract was filled), the content of various sections of the intestine was examined histologically. I tied off various parts of the central and lower intestine so that their content could be studied separately. The results were as follows:

a) Pharynx, esophagus, and proventriculus are usually free of food particles. The food is presumably conveyed very rapidly by the observable peristaltic motions of the esophagus and by the sucking motions of the pharynx and proventriculus into the greatly expansible intestine.

b) Upper and middle intestine (Figure 55a,b): Tissue fragments and isolated cells.

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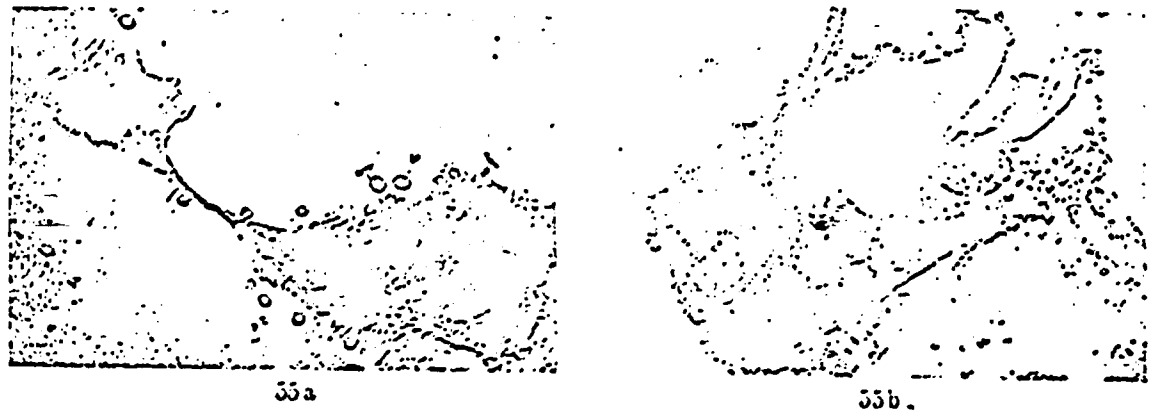

55a 55b.

Figure 55. Fragments of tissue of a Gerris in the upper and middle intestine of a) a Lamyris larva and b) a Phymata larva.

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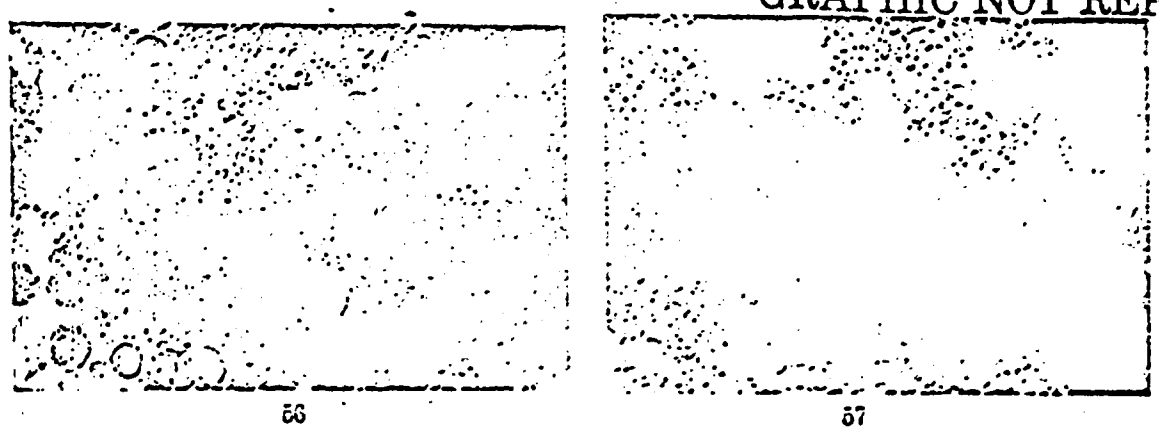

56 57

Figure 56. Cell nuclei in the lower part of the middle intestine and the upper rectum, with the cytoplasm already digested. Increase in finely granulated, completely digested chyme.
Figure 57. Homogeneous finely granulated, completely digested content of the middle to lower portion of the lower intestine.

c) Lower middle intestine and upper rectum (Figure 56): Isolated cells and cell nuclei completely liberated from the cytoplasm; increase in finely granulated, completely digested content.

d) Central and lower portions of the lower intestine (Figure 57): homogeneous, fine-grained, fully digested content.

3. The middle intestine possesses a peritrophic membrane, which is said to be lacking in extraintestinally digesting insects (Weber [134]).

II. On the Question of Poison Effect on the Prey

In the larvae's attack on shelled snails the snail withdraws into the shell at every bite, and the further pro-

usually remain hidden. That after one or more bites and after powerful mechanical stimuli the snail's foot is no longer quite retracted into the shell, and that the larva at about the same time stops the attack gives grounds for conjecture that the snail has been injured in a way that endangers its life.

In shell-less snails all that is observed externally is a progressively decreasing capability of motion of the animal, which has previously been defending itself violently, down to the point of complete motionlessness. During the attack apart from body movements only the cardiac motions are clearly observable. In the case of transparent shells they can be seen directly, and in other cases carefully making an opening in the shell does not disturb the cardiac action.

1. Cardiac motions of the snail during the attack. The slightly increased cardiac frequency observable in a Cornea hortensis with an artificial opening in its shell remains constant after a few minutes. The experiments do not begin until after that. The normal cardiac frequency of Cornea when crawling fluctuates between 60 and 75 beats a minute, that of the snail resting, with its shell closed with a membrane of slime, is between 30 and 60 a minute at room temperature.

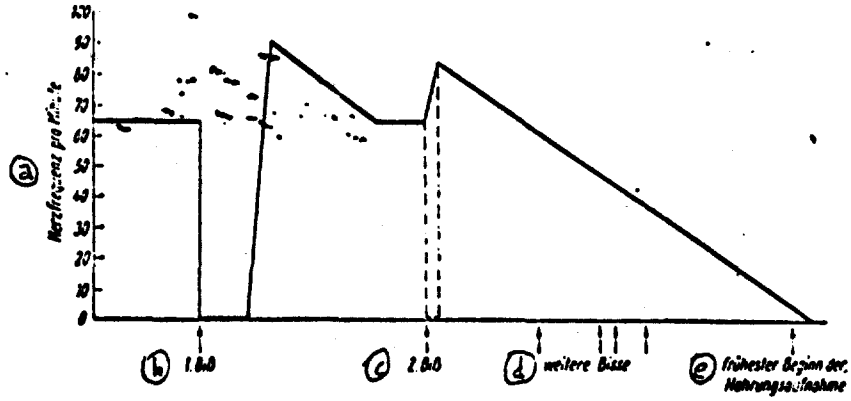

Figure 58. Example of the variation of the cardiac frequency of a snail (Cornea hortensis) during the attack of a larva. Explanation in the text. a) Cardiac frequency per minute, b) first bite, c) second bite, d) other bites, e) earliest beginning of feeding.

An example of the cardiac frequency curve is shown in Figure 58. The chronological course (abscissa) naturally cannot be set down in units, since the sequence of bites is inconstant both chronologically and quantitatively. Since the physiological conditions (stock of poison) and the ratio of

size of larva to size of snail vary, individual observations cannot give a general picture. I shall limit myself to a summarizing discussion of the general characteristic phenomena.

The cardiac frequency curve follows the same pattern in all experiments: Failure of heartbeat after the first (and occasionally after the second) bite, followed by a pause [illegible] and then during other bites, after which the heartbeat [illegible] not falter, a gradual decline to a final standstill. In individual cases, of course, there are other variations in the cardiac motions not shown in the figure. When the cardiac frequency has declined to about 1/2 the normal rate the first disorders set in. The amplitude is diminished, the heartbeat becomes more and more irregular, sometimes spasmodic, the atrium discontinues its activity and is moved passively by the peristaltically vibrating motions of the ventricle. Often the reverse phenomenon occurs in the sequence; the ventricle comes to a stop and the auricle moves. Within the pericardium the peristaltic contraction-and-dilatation phases run in constant alternation from back to front and back again. At low frequencies, below about 20/min, a dilatation is followed by a convulsive, violent contraction, then perisystole, which may last a varying length of time. When the movement of both parts of the heart ceases entirely, for a certain time there still remains a vibratory motion within the pericardium, without amplitude.

For diagnosis and to take account of possible damages, in the series of experiments described below the symptoms of the cardiac motions were always noted.

The phenomena described occur e.g. in a Cepaea hortensis of 6 mm shell diameter after the first bite of a full-grown hungry larva. If immediately isolated the snail dies within one day (no heartbeat; it can be easily pulled out of the shell without resistance). Snails with a shell diameter of 15-20 mm usually are not viable after 4 to 6 bites of a hungry full-grown larva. In these cases the heartbeat persists even after complete paralysis of the motor musculature of the body (no reaction to pinpricks). Full-grown Cepaeae are often overcome only after days and after dozens of bites (cf. 3).

2. Experimental Mechanical Attacks on the Snail's Body

a) Upon pinching with a strong, sharp-pointed pair of pincers in various regions of the body (especially in the fore end), shelled snails withdraw into the shell and shell-less snails defend themselves as when bitten by larvae, with secretion of slime. After several dozen repeated violent pinches the snails show no defects in mobility and no effects dangerous to life; the cardiac frequency, which normally goes up (by 1/4

to 1/3) upon withdrawal into the shell, returns to normal after some seconds, or at most minutes.

b) Snails (Cepaea ___) were pierced completely through with a sutor; needle [illegible] in diameter. The punctures were made successively in the snail in the following regions of the body (a typical example):

1. Puncture through the tip of the foot: 78/min; does not completely withdraw into the shell, goes on normally.

2. Puncture through the middle of the foot, partially through the viscera: 68/min, complete withdrawal into the shell; closes it with membrane of slime.

3. Puncture through the base of the eye tentacle (horizontal): 85/min, immediate withdrawal into the shell; comes back out after a few minutes.

4. Puncture behind the feelers (near the cerebral ganglion): 72/min, immediate withdrawal into the shell.

Snails mistreated in this way live on for weeks with normal cardiac frequency, and normal mobility, and form a membrane of slime at the entrance to the shell (as a snail injured by the attack of a larva never does).

c) Fore ends cut off close behind the mantle (Limax arrestis) often continue to move for hours without sign of disturbance and with good coordination. The rear end, without ganglia, is incapable of any locomotion.

Other severe injuries (see below) are survived for hours and days without damage to the motor mechanism.

Mechanical stimuli and massive injuries which are incomparably greater than the mechanical effect of bites with the mandibles are without influence on the locomotion and cardiac activity of the snails, and in fact usually do not affect their vital phenomena (except as in 2c) at all.

3. Stock of Poison

a) If the snail just paralyzed (or killed) is replaced with a live one, the larva (Lampyris) is no longer capable, even after many bites (over 50), of overcoming its prey. Cardiac frequency and capacity for movement remain normal; disturbances are only as described under 2.

b) The stock of poison is exhausted after 4 to 5 bites. Even small shelled snails which are mortally injured with one bite, or shell-less snails, which react extremely sensitively to bites of larvae, endure an attack lasting hours without injury; they are still living weeks afterward. -- That full-

grown cepaeae often cannot be fatally injured and overcome [illegible] presumably due to the small stock of poison, and perhaps also to the fact that the poison cannot be injected deep enough in the thick skin of old snails at every bite.

c) After about 12 to 30 hours the bite of the larva again has its effect; the stock of poison appears to have been regenerated (test with the larvae of b).

4. Place of Production of the Poison

Crushed matter and extracts from various parts of hungry Lamprys larvae were injected into the fore end of the snails. (For each individual test 10 shell-less and 10 shelled snails of various species and sizes were used.) Extracts were obtained by crushing the corresponding parts of the larva in a mortar with double-distilled water. Control injections with pure double-distilled water in the fore end of the snails were without influence on the vital phenomena of the snails; they behaved like uninjected control snails. Experiments a to d were repeated three times.

a) Extracted crushed material of whole larvae: Shell-less snails were dead after 2 to 6 days, shelled snails after 9 to 17 days. (Here and in the following cases the first number indicates the time of death of the first snail, the second that of all snails used in the experiment.)

b) Content of intestine and extracted crushed material from the intestines: Shell-less snails were dead after 2 to 6 days, shelled snails after 6 to 12 days.

c) Head extract: Shell-less snails dead after 2 to 7 days, shelled snails after 4 to 10 days.

d) Hemolymph: Shell-less snails dead after 1 to 3 days, shelled snails after 4 to 9 days.

e) Intestinal secretion injected into other parts of the body, e.g. visceral sac, foot, and pericardium, had no fatal consequences. These experiments could be carried out only once, on one Cepaea hortensis, for lack of larvae.

f) I repeated experiments b) and c) using an earthworm. When intestinal secretion was used the earthworm was dead after 2 days, when head extract was used it was killed immediately!

These experiments show firstly that all the extracts obtained from the larvae have a poisonous and in the final result a fatal effect on snails, secondly that the poisons from different parts of the body work equally well, and thirdly that shell-less snails, as in natural capture of prey, are much

more sensitive to larval poison than shelled snails. -- Any differences in the poisonous effect of the various extracts can be determined by considering the snails' symptoms in detail. Thus the extracts from intestine, head, and whole larva and the hemolymph in that order had an increasingly powerful and rapid effect on the locomotive mechanism of shell-less snails; in the case of shelled snails only the hemolymph had an early injurious effect on the locomotion, while the other poisons seemed to leave no outwardly visible damage during the first few days at all. In these experiments it must be borne in mind that the concentrations of the extracts were bound to be very ununiform depending on their origin; the tiny head naturally yielded the least substance.

The occurrence of substances poisonous to snails in so many different parts of the larva was not to be expected. The question now is what poison is injected into the snail through the mandibular canals of the larva, how it is connected with the mandibular canals, and where it is stored. We must still assume the storage of a small stock of poison, for this stock is demonstrably exhausted after only a few bites with no visible outpouring of liquid. The intestinal secretion is the last thing to assign the responsibility to, since it is secreted for hours at a time during the intake of food (which see) and because it has the least effect on the snails.

3. Discussion

Little is known concerning the biological significance of the rhythms and the time sense in the life of the larvae; occasionally this has been related to the search for food (von Buddenbrock [24], Welsh [139]). The circumstances of the activity of larvae of lampyridae allow of such an interpretation, for both the annual and diurnal rhythm of activity (Frömming [42], Jaeckel [66], Szymanski [124]) and also the preferred environment of most snails coincide with the corresponding environmental demands and habits of life of the larvae. For the larvae cannot overcome a shelled snail sealed up during its hibernation with a thin membrane of slime. A definite rhythm of feeding, however, is ruled out by the fact that the larvae can do without food for months. That optically oriented animals have a monophasal diurnal activity variation and tactile, osmatic animals a polyphasal one (Szymanski) does not hold for my tactile, osmatic larvae, for they have a definite monophasal activity cycle. This can be explained by the fact that it is not the diurnal microclimatic variations of the stratum of air near the ground that determine the variation in activity, but, apart from endogenous factors, solely the diurnally varying conditions of light and darkness.

The endonomic rhythm of luminescence of the larvae is inexplicable. They glow neither to defend themselves from enemies nor to attract their prey.

The whole nature of the predatory behavior, the morphological adaptations to the snail diet, and the fact that [illegible] snails can survive much grosser injuries tell in favor of the view that the larvae of both species do not overcome their prey purely mechanically, but poison it. The poison must work fast, for fleeing snails (especially species of Limax) can simply run away from the larvae, which follow the trail of slime slowly and gropingly. That the larva concentrates its attack on the fore end of the snail and not on the rear, which it reaches first in pursuing the snail, is no doubt an indication that the poison must work on the nervous system of the snail, which is concentrated at the fore end. A further indication of poisonous effect on the central nervous system is the long continuing action of the snail's heart, whose relative independence from the central nervous organs is well known (Skramlik [118,119], Willems [141]), after paralysis of the whole bodily musculature. The great secretion of slime induced by the bites may contribute to impairing the locomotion (Bronn [12]), since the snail is afterwards unable to form the slime track on which it must crawl; for the locomotor undulations may still be continued without the snail's being able to move about. (This can be readily observed in shell-less forms.) The bites of the larvae do not act as a "desensitizing anesthetic" from the effect of which the snail recovers (Fabre [40]); they are lethal. Vogel's assumption [127,129,131] that the toxic effect comes from expectorated intestinal secretion, as in the case of extraintestinally digesting beetles, cannot be correct, for the stock of poison is exhausted after a few bites without visible efflux of fluid, although the larvae are supposed to have the intestinal secretion available for more than two days afterwards for the "extraintestinal digestion"! But according to Vogel's and according to my own studies the mandibular canals appear to be connected only with the oral cavity (and of course by way of it with the intestinal tract). In my injection experiments it is conspicuous that the extract of the tiny head has lethal effects that are disproportionately more powerful in comparison to the higher concentrations of the abundant intestinal extract. That justifies the assumption that there is in the head of the larvae a small, quickly exhausted poison-producing or poison-concentrating apparatus, such as Vogel himself might have found to the number of four in the anterior bases of the pharynx. He interprets these, of course, as organs of taste. But these structures, described by him as pouch-shaped complexes of cells with markedly vacuolized content (!), in view of their glandular nature, hardly

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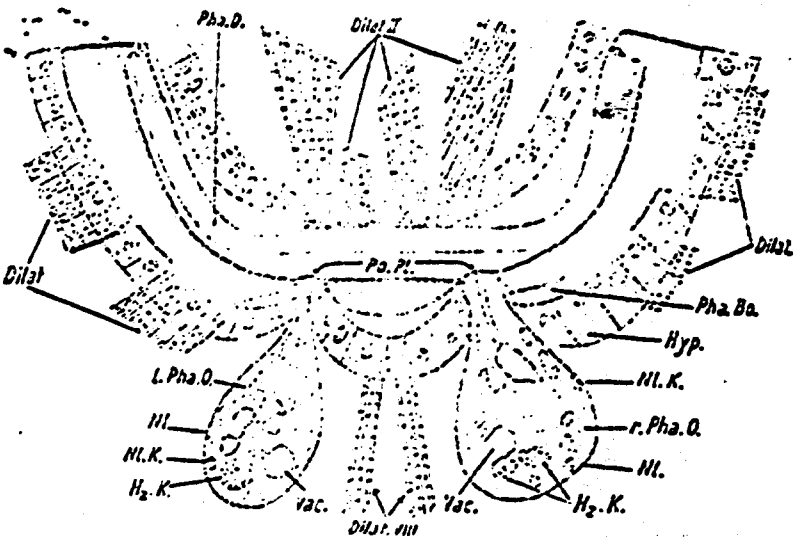

Figure 59. Vogel's "pharyngeal organs of taste" (from Vogel [128], page 395). Cross section through the anterior part of the pharynx and one pair of the pharyngeal organs of taste. Fixative: absolute alcohol. Staining: eosin-hem. Legend: Dilat., dilatators of the pharynx; Hz.K., nuclei of spiral cortical cells; Hyp., hypodermis; l.Pha.O., left pharyngeal organ; Nl., neurilemma; Nl.K., nucleus of neurilemma; Pha.Ba., base of pharynx; Pha.D., roof of pharynx; Po.Pl., sensillae placodae of the pharyngeal organs; r.Pha.O., right pharyngeal organ; Vac., Vacuoles. Zeiss ocular 2. H.Imm. 1/12. Zeiss apparatus.

suggest sensory cells (Vogel [129], page 395, Figure 59). [Sic; cf. "[128]" with the same page reference under Figure 59 above.]

Through the bases of the mandibles, situated forward toward the entrance to the pharynx, an easier communication of the mandibular canals with the pharynx is achieved. Because of this important specialization the mouth opening of the larvae of lampyridae is relatively very small. This calls for a good pulverization of the food, which (according to Vogel, too) can be accomplished splendidly by the mandibles. Aided by the peculiar location of the hair-covered parts of the mouth organs and by the suctional function of the pharynx and perhaps also the proventriculus, the normal transport of undigested food has no obstacles in its way. According to Haddon's [51] and Vogel's portrayals the bristle arrangements on the mouth parts serve as a sieve apparatus which prevents the entry of solid food particles into the oral cavity. It is evidence against the filter effect that pieces of food are taken and that whole snail radulae that are larger than the unexpanded mouth opening

are found in the intestine. The sieve mechanism could be explained only if we conceived of the entire equipment of the mouth as a stationary sucking apparatus and left out of account the typical moving action in the living specimen, which has up to now been largely disregarded.

Haddon makes no statements about a possible extraintestinal digestion, but Vogel interprets his [illegible] morphological findings in that light, drawing his conclusions as a morphologist, without attempting the difficult direct observation. It is significant that Fabre and Vogel speak of extraintestinal digestion only in connection with a diet of shelled snails. By virtue of their shells they are conceivably quite well suited to that scheme; the entire snail is supposed to be "liquefied" simultaneously in the shell into a "bouillon" (Fabre) or to a "tough, viscous broth" (Vogel). But the larvae of the lampyridae also eat shell-less snails and other (shell-less) animals just as readily! Direct observation shows that the already chopped food disappears immediately and relatively quickly into the oral cavity, so that it is subjected to the digestive juice much too short a time to be "digested" before being taken into the intestinal tract. The histological examinations of the chyme from the oral cavity and from the intestinal tract confirm this and refute Vogel's histological findings. The mode of function of the mouth parts and of the pharynx and also the consistency of the food offer none of the necessary prerequisites as assumed for extraintestinal digestion <u>generally</u> (Jordan [67], von Lengerken [72]). Moreover the larvae of the lampyridae lack various adaptations or characteristics typical of extraintestinally digesting insects, such as diverticula especially of the lower part of the middle intestine for absorption of the liquefied chyme and isolation from the intestinal lumen and so from the digestive secretion and a minimal defecation as a result of the almost total resorption of the preorally liquefied chyme (Blunck [7]). A peritrophic membrane, lacking in such cases (Weber [134]) is present in the larvae of the lampyridae. The larvae do, however, eliminate a secretion at irregular intervals during the intake of food. This is not eliminated through the mandibular canals with the mandibles closed, as during the attack, -- a thing that is quite visible in biting into elderberry-pith dummies, and occasionally also with mechanical and chemical stimuli, -- but through the mouth opening with the mandibles opened. But it will be clear from what has been said that this is no extraintestinal digestion in the measure described by Fabre and Vogel; in this secretion (presumably from the intestine) I see rather a "salivation" of the food, the transport of which and its sucking into the pharynx are thereby facilitated.

To solve the question of the place of production and [illegible] of the poison definitively, however, would require additional precise histological studies.

B. Sexual Biology (Sensory Physiology, Sexual Behavior)

I. Sexual Characteristics Concerning Luminescence and Sexual Behavior of the Lampyridae

Luminous organs with intracellular luminescence occur in all developmental stages of the native and foreign lampyridae so far investigated (though occasionally hidden by pigment in the males). Buck [23] distinguishes four types of light emission in fireflies: 1. continuous glowing, 2. intermittent glowing, 3. pulsation, and 4. flashing. The glowing of the eggs of our lampyridae corresponds to type 1; I put the larvae and females of both species with type 2, while the luminescing Phausis male would belong to the third type. The American lampyridae and the south-European Luciola species belong to the fourth type [see Note].

[Note] Based on my own observations of Luciola lusitanica and Luciola italica.

Opinions differ as to the biological significance of the luminescent capacity of the imagines. The following statements are to be found in the literature: 1. Luminescence and sexual dimorphism (of the luminous organs, eyes, wings, antennae) are attuned to each other and serve to enable the sexes to find their way to each other (Bongardt [10], Exner [39], Knauer [68], Morley [94]); 2. Luminescence and sexual dimorphism are in conflict (Anon [4], Gorham [49], Olivier [96,97] and so do not belong to the sexual behavior at all; 3. Luminescence serves other purposes in addition or exclusively (Anon [4], Blair [for exact reference see Harvey, 55], von Bronsart [13], Czepa [31,32], Dieckhoff [34], Gorham [49], Haupt [57], Hess [58], Höllrigl [62], de Kerville [for exact reference see Harvey, 55], Macaire [76], Olivier [96,97], Perkins [101], Seitlmeier [137,138], and Wielowiejski [140]).

Despite the enormous literature and the diversity of opinion, with regard to our native lampyridae there are no experiments on the sexual biology and no detailed comparative studies on the sexual dimorphism. The results of experiments on foreign lampyridae by Emery [37,38], Mast [82], McDermott [85-88], and Buck [19-21] give unmistakable evidence of a connection between luminescent power and sexual behavior and have since been accepted and generalized for all lampyridae in both German and foreign literature, regardless of the widely varying structure and differing behavior of those species as compared to our native ones (cf. Chapter D III).

There were thus the following questions to be clarified: 1. The normal sexual behavior of the two species, 2. the behavior with respect to light, 3. structure and biological function

of the eyes in comparison of the males and females of the two species, 4. analysis of the "female pattern" of the two species occurring simultaneously in the same biotope.

1. Normal Sexual Behavior in Lampyris noctiluca and Phausis splendidula in the Natural Habitat

Observation of the normal behavior of the two species in their natural habitat was the starting point for the experimental part of the studies of the sexual behavior.

a) Day-Night Rhythm of Activity and of Luminescence

Males and females of both species appear throughout their lifetime (females as a rule only until fertilization) every evening at the coming of darkness, i.e. between 8:00 and 9:30 p.m. The males (definitely verifiable only for the luminescing Phausis males) do not fly until about 30-60 minutes before the females begin to glow, but are active before that time simultaneously with the females. Each individual female leaves her hiding place at a fixed time, within a range of 5, or in exceptional cases 10-15 minutes. Just as constant times of appearance are given by Mast [82] and Buck [20] for Photinus pyralis. The female assumes a definite posture for glowing (cf. appetency behavior) and remains in that posture until toward midnight, in rare cases an hour or two longer. During the last few days before death the female, after assuming the glowing posture, runs around in a circle of about 50 cm in radius, only to glow again afterwards in the typical posture. This procedure may be regularly repeated in the course of the evening at intervals of 10-20 minutes. Glowing after midnight probably is connected with the maximally accumulated sexual drive toward the end of the lifetime; I have rarely seen it. The time of disappearance of the females is not as sharply fixed individually as their appearance. My decoy experiments (which see) also confirm the limitation of the absolute activity phase (not only of the "swarming") to 11:00 or at most 12:00 p.m. In Phausis males I observed toward the end of the activity period more or less vigorous scratching or digging motions, performed with the legs and the lowered prothorax. As a rule the males stop flying 30-60 minutes earlier than the females stop glowing. With the beginning of activity both sexes of Phausis and the Lampyris female begin to luminesce. The rest of the time -- after midnight and during the day -- the imagines are in hiding, in fallen leaves, in the matting of grass roots, under stones and the like; they are completely inactive and do not luminesce unless they are disturbed or are in the premortal state. Where some investigators have found a more or less powerful glow during the day they must have had the last-mentioned cases before them.

The natural rhythm of activity and of luminescence is largely independent of weather conditions such as temperature, atmospheric humidity, wind, rain (but cf. Newport's, Mast's, and Buck's observations on American lampyridae). I was able to discern a dependence on the weather only in the intensity of activity and not in the rhythm itself, namely that [illegible] especially the males are very sluggish in cold [illegible] and [illegible] were not [illegible] (Table 14). The influence of the [illegible] cloudiness or of the light intensity (:) is shown by Table 14 and more objectively by Chapter D I 2c. Divergent observations concerning the reported normal course of the rhythm of activity and luminescence have been made by Maire [76] and Bongardt [10], who saw Lampyris females glowing until daybreak. It might be assumed that the insects involved in this observation were larvae, which do glow until dawn; for otherwise the observations -- even of foreign lampyridae -- agree on this point with mine: Allard [cited in Harvey, 55], Buck [20], Hess [58], Mast [82], Newport [95], Verhoeff [126], Weber [136], and others. There is an interesting exception in the imagines of Pyropyga fenestralis Mols., observed by Hess, which in contrast to their larvae have neither luminous organs nor a nocturnal activity, but are pronounced daytime animals.

b) Sexual Appetency Behavior

What follows is chiefly a discussion of the modes of behavior during the above-mentioned periods of activity and luminescence, which finally lead to or induce copulation. The sexual appetency behavior is largely the same in the two species.

The sexual appetency behavior of the male during his activity phase consists essentially of a swarm flight and the preliminary activities connected with it. After leaving his hiding-place the male makes an effort to climb up on all objects projecting above the ground; the elytra are carried somewhat spread laterally and hanging down a little. When the end of the object is reached the real preparations for flight begin: wide-angled spreading upward of the elytra, unfolding of the alae with the aid of the prehensile tip of the abdomen, which is curved high under the wings for the purpose, and start. The horizontal speed of flight (observations chiefly of the Phausis male, which luminesces and is therefore easier to observe) is hardly greater than 1 m/sec, and on the average only 30-50 cm/sec or even slower. The flight is carried out at a low altitude of 0.50-2 meters above the ground and is largely dependent on the terrain or its plant cover. Generally in case of uniform plant cover (e.g. greensward) an average altitude of 1 m is maintained. Light contact with an object triggers a

Table 14. [illegible] table shows the starting and stopping times of luminescence and the climatic conditions, as well as temperature and humidity on the basis of quarter-hourly observations. For lack of space I can give the data for only one ♀, choosing for the purpose one that I was able to observe throughout the whole life span in the natural biotope.

Date	Luminescence: beginning	Luminescence: stop	Weather	Check	
2. 8. 1958	21^{02}	22^{15}	N = 2; W = 1/W	Kontrolle Temp. ° C %	21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 11,3 11,5 11,9 12,6 13,4 13,4 13,6 13,4 13,5 13,5 13,5 const. 100%
3. 8. 1958	21^{03}	22^{10}	N = 0; W = 4/W	Kontrolle Temp. ° C %	20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 13,2 13,2 13,2 13,4 14,0 14,0 14,4 14,7 14,7 14,8 const. 100%
4. 8. 1958	20^{58}	23^{30}	N = 0; W = 4/WSW	Kontrolle Temp. ° C %	20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 23^{45} 24^{00} 14,1 14,0 14,0 14,0 13,6 13,4 13,0 13,0 13,0 12,7 12,5 11,8 11,8 11,8 const. 100%
7. 8. 1958	21^{05}	23^{45}	N = 1 → 4 (um 22^{30}) S; um 22^{30} = 2, um 23^{30} = 4, R; W = 4–5/W	Kontrolle Temp. ° C %	21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 14,1 13,0 13,0 13,3 13,5 13,5 14,0 13,8 12,7 13,5 14,2 const. 100%
8. 8. 1958	21^{10}	22^{30}	N = 4; W = 4–5/W	Kontrolle Temp. ° C %	20^{30} 20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 23^{45} 24^{00} 24^{15} 17,2 17,2 17,3 16,9 17,3 17,5 17,7 17,3 17,3 17,1 17,3 17,3 17,3 17,3 17,3 17,3 92%
9. 8. 1958	20^{50}	23^{00}	N = 4; W = 3–4/W	Kontrolle Temp. ° C %	20^{30} 20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 23^{45} 24^{00} 24^{15} 20,5 20,5 20,0 19,5 19,6 20,2 20,2 19,7 19,8 19,3 19,5 19,2 18,9 19,1 19,1 19,0 98–100%
10. 8. 1958	21^{00}	24^{07}	N = 1, bis 23^{30} = 4, S; W = 0	Kontrolle Temp. ° C %	20^{30} 20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 23^{45} 24^{00} 24^{15} 24^{30} 24^{45} 1^{00} 1^{15} 21,2 21,0 20,5 20,3 19,8 19,5 19,2 19,2 18,9 19,0 19,0 19,1 19,3 19,4 19,2 19,3 19,2 19,3 19,2 19,2 const. 100%

Signs and Abbreviations:
R - rain, S - shower, [illegible] - heat lightning, F - distant storm (more than 3 km away), [illegible] - storm close at hand, % relative humidity, Temp. - temperature, _ increasing until, _ decreasing until, N - cloud cover, 0 - cloudless, 1 - 1/4 overcast - clear, 2 - 1/2 overcast - somewhat cloudy, 3 - 3/4 overcast - cloudy, 4 - 4/4 overcast or completely overcast, W - wind (followed by wind force on the 12-point Beaufort scale and by direction). [German words on table: for um read at; for bis read until; for Kontrolle read time.] Continued on page 91.

Table 14 (continuation). For the meaning of signs, abbreviations, and German words appearing in the table, see the footnote on page 90. [For ab read beginning; for dann read then; for gegen read toward.] Sudden changes in temperature are attributable to changing weather conditions.

Date	Start	Stop	Weather	Check	
11. 8. 1958[1])	20^{05}	21^{00}	N = 4, ↓ ab 17^{00}, R, W = 7--8	Kontrolle Temp. ° C %	20^{00} 20^{05} 20^{10} 20^{15} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 19,5 19,4 19,3 19,2 18,8 18,5 18,2 17,5 17,3 const. 100%
12. 8. 1958	21^{10}	23^{10}	N = 4, R (bis 22^{00}); bis 23^{00} = 3, dann 4, R; W = 3 -4/W	Kontrolle Temp. ° C %	20^{00} 20^{05} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 23^{45} 14,3 14,3 14,3 14,8 14,5 14,2 13,5 13,5 13,0 13,3 13,5 13,7 14,0 14,0 const. 100%
13. 8. 1958	20^{55}	22^{50}	N = 3 (bis 21^{00}), ab 21^{00} 5 = 0; W = 1/W;	Kontrolle Temp. ° C %	20^{00} 20^{15} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 23^{30} 13,7 13,8 13,6 13,5 12,5 11,7 11,5 11,6 11,2 11,0 11,0 11,2 11,2 const. 100%
14. 8. 1958[2])	20^{15}	22^{25}	N = 4, S -> R; W = 3--5;	Kontrolle Temp. ° C %	20^{00}--23^{00} const. 18,0 const. 100%
15. 8. 1958	20^{12}	23^{10}	N = 0; ab 22^{00} -> 1; W = 0;	Kontrolle Temp. ° C %	20^{15} 20^{30} 20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 17,6 17,6 17,5 17,5 17,3 17,2 17,0 17,5 17,6 17,8 17,8 17,7 18,0 const. 100%
16. 8. 1958	20^{37}	22^{55}	N = 1; W = 3 -4/W	Kontrolle Temp. ° C %	20^{15} 20^{30} 20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 16,9 16,7 16,3 16,3 16,0 15,5 15,5 15,3 15,1 14,8 14,6 14,5 14,3 const. 100%
17. 8. 1958	20^{25}	22^{50}	N = 2; W = 0;	Kontrolle Temp. ° C %	20^{00} 20^{15} 20^{30} 20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 23^{15} 15,6 15,5 15,4 15,6 15,5 15,5 15,5 15,5 16,4 16,5 16,5 16,0 15,7 15,3 15, const. 100%
18. 8. 1958[3])	20^{26}	22^{58}	N = 3 -> 4 (gegen 21^{30}) ↑, S, ab 23^{00} R; W = 0 -> 3	Kontrolle Temp. ° C %	20^{00} 20^{15} 20^{30} 20^{45} 21^{00} 21^{15} 21^{30} 21^{45} 22^{00} 22^{15} 22^{30} 22^{45} 23^{00} 20,5 20,5 20,4 20,0 19,8 19,7 19,5 19,5 19,5 18,1 18,5 18,7 18,9 const. 100%.

1) At 17:00 a severe storm begins with pouring rain; at 20:00 it becomes clearer again, as at 21:00 the day before. -- The early disappearance is to be attributed to the fact that lightening provided a light almost as bright as day between 21:00 and 22:00. (1000 flashes counted in 50 minutes; photographs taken by the light of the lightning showed that the females had given up their glowing posture!!)

2) From 14 August 1958 until end of life (18 August 1958) signaling every evening in the glowing posture (cf. Chapter D I 1).

3) The female was out of her hiding-place at 20:15, took the first glowing posture at 20:26 and began to glow, left the exposed glowing position about 8 times in the course of the evening; glowed there for several minutes in normal posture; at 22:58 leaves the glowing position with decreased luminous intensity, where she had been since 22:45, and a few minutes later is swimming in water because of a heavy rainstorm. The female was put into a glowing dish, laid 27 unfertilized eggs and died toward morning of 19 August 1958.

clasping reflex of the tarsi and the flight ends. (Method of catching the males easily without equipment!)

If the male comes to a female in the open or to a decoy in the flight cage, he drops suddenly and almost vertically from a height of at least 1 meter and meets the female with great accuracy. For experimental investigation of this diving landing, glowing females were put into a glass cylinder 9 cm in diameter and 15 cm high. Over 65% of the flights ended inside the cylinder, the rest in a circle of at most 20 cm outside it. (Cf. eye investigations, Chapter D I, 3.) After an inaccurate flight the male runs toward the female with very hasty movements (not otherwise customary); if the sight is obstructed by ground plants, he immediately climbs to an exposed point and flies toward the female from it. The last case may be repeated, or combined with the first, depending on the circumstances, or it may, presumably because of sight difficulties, still not lead to union with the female flown toward, even after a running about of varying length and executed with hurried movements; then the male suddenly flies away. -- In the diving flight the elytra and wings must be folded quick as a flash into the rest position, for even in landings from low altitude (about 20-30 cm) they are in the normal position on the back when the insect strikes the ground. More rarely a spiral path of flight is observed, which is probably to be attributed to imperfect folding of the wings.

During the searching flight the Phausis male glows strongly and continuously, but with somewhat fluctuating intensity. (Lampyris males glow, but hardly visibly; cf. pages 45-46.) The statements that crop up everywhere in the literature about an irregular flashing of the males must be due to inaccurate observations, for if one follows the flight from normal observational perspective (standing), the ventral luminous organs of the males, which are for the most part flying lower, are repeatedly covered by the abdomen. In addition the restless up-and-down flight hinders a continuous line of sight to the luminous plates. If the observer lies on his back he can easily assure himself in clear weather as to the continuity of luminescence during flight. -- It is only when leaving his hiding-place and climbing to a take-off point, and again after a landing, that the male shows an irregularly fluctuating glow, which usually does not attain the intensity usual in flight.

The flight is a quite typical and pronounced lifting flight. The abdomen, which is relatively mobile for a beetle (in Lampyris males longer than the elytra!) hangs down almost vertically in flight, the tip of the abdomen usually curved forward a little in the ventral direction. The position of

the center of gravity conditioned by this posture (center of gravity behind and below the point of attachment of the wings) retards progressive motion, but promotes the "dipping" flight also observed in American fireflies (McDermott [83]), which apparently can be even be regulated by movements of the abdomen. With movement of the abdomen into the vertical position the flight becomes on the whole less suited for horizontal motion and more favorable for vertical maneuver.

In the female the following takes place during the period of "activity" and luminescence: Not shining or only slightly glimmering (mostly with the larval organs), the female leaves the daytime hiding place to seek out an exposed, elevated place (stone, blade of grass, or the like). If a female is put on a flat surface, she hunts until she finds such a suitable place, often tries over an hour to climb up a glass wall, and accepts any object introduced immediately as a her glowing place. The glowing posture is typical, and though it is executed differently in the two species, it is such that the ventral luminous organs are turned upward. The most usual glowing posture of Lampyris females is like the normal walking posture with the difference that the abdomen is twisted like a screw in the lengthwise axis by 90 to 180°, so that the luminous organs beneath the sternites of the posterior abdominal segments are turned upward and the corresponding tergites downward. At the

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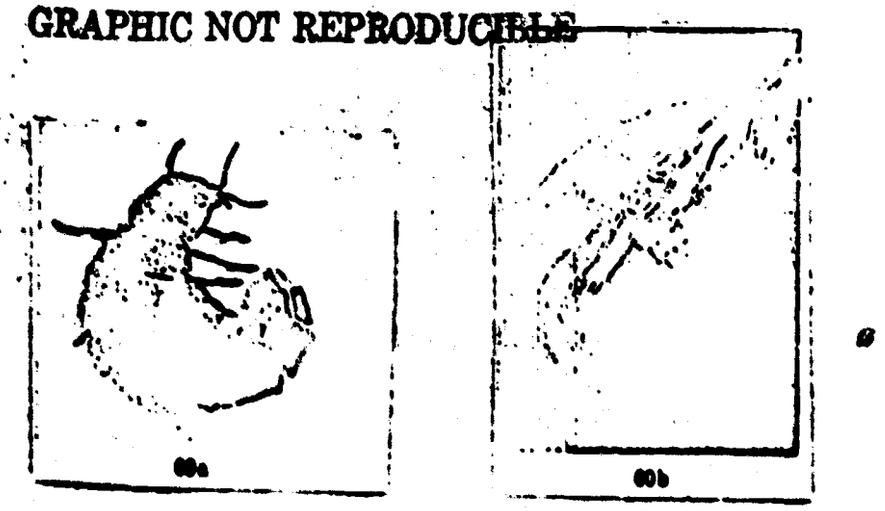

Figure 60. Glowing postures of the Lampyris female, on more or less plane elevated places (a) and on more or less vertical objects (b).

same time the tip of the abdomen is thrust upward slightly to the side (Figure 60a). On thin vertical objects the spiral dislocation of the abdomen is occasionally lacking or imper-

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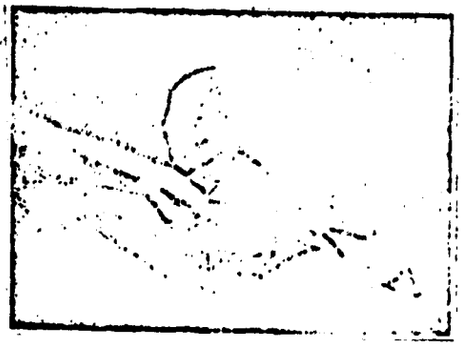

Figure 61. Glowing posture of the Phausis female.

fectly executed; the female, clinging to the object with her head up, bends the abdomen in the ventral direction more or less at a right angle, so that in this case too the luminous organs are exposed upward (Figure 60b). -- Phausis females in all cases merely curve the tip of the abdomen upward from the normal walking posture; occasionally the entire body is diagonally inclined upward toward the back from the support (Figure 61). This makes not only the ventral imaginal luminous plates but also the dorsally visible larval luminous bulbs effective. The females of both species, if undisturbed, remain motionless in their glowing places, glowing continuously with maximum intensity, until the end of the daily period of activity. This very continuity of luminescence in the females of the two species is a quite fundamental difference in the sexual behavior as compared to the American and South-European (Luciola) species. If Lampyris females are disturbed by mild mechanical or luminous stimuli, the glowing posture is given up and the luminescence decreases depending on the intensity of the stimulus down to a weak glimmer, but after a short time -- even in the case of repeated disturbances -- the complete glowing posture is resumed. After powerful stimuli or when disturbed toward the end of the period of activity and luminescence the female crawls away and hides and does not reappear on the same night. -- The Phausis female is far more sensitive. A mere breath or a vibration can upset her so that she crawls away and hides and does not appear again on the same night. -- The normal end of the period of activity and luminescence is signaled by females of both species by giving up the glowing posture, gradually reducing the luminous intensity (the larval organs as a rule retaining their bright glow longer in the case of Lampyris, the imaginal organs in Phausis), and seeking the hiding place. Most of them choose the same hiding place again, although they have innumerable similar refuges available nearby.

In conclusion an interesting intensification of the female appetency behavior should also be mentioned. Unfertilized Lampyris females toward the end of their lives, while largely retaining the normal glowing posture, make beckoning or rotating movements of the abdomen, and at the same time the external genital appendages, which are otherwise enclosed by the terminal segments, are protruded and retracted with circular motions at arrhythmic intervals. In "old" females of both species it is also noticeable that they occasionally give up the glowing posture several times in an evening, run about restlessly, and begin to glow again at a different place. Both these phenomena are doubtless expressions of the heightened sexual appetency behavior.

Bongardt [9,10], von Bronsart [13], Höllrigl [62], and Knauer [68] report that they have found females (at least of Lampyris) lying on their backs, and they interpret this as a special evidence of the sexual nature of the luminescence. I cannot confirm this. Of the far above 200 females of the two species that I have observed outdoors and in the laboratory, I have never seen one lying on the back. It is evidence against this that the females never willingly relinquish the contact of the tarsi with the object they are resting upon, that when placed on their backs they always immediately execute turning movements (Chapter E II 5), and that copulation with a female fastened in position with the back down never succeeds even after attempts at copulation on the part of the male for over an hour. With females in the normal position copulation takes place in a very short time, even in the case of dead females. (On this point cf. the next chapter.)

c) Copulation

The following applies to both species if not otherwise specified.

In immediate proximity to the female the behavior of the male changes. The movements become more hurried, almost unsteady, and the antennae are moved violently and rapidly. As soon as the male touches the female, the female gives up the glowing posture. The male, vibrating fast, immediately mounts the female regardless of which direction he approaches her from, and thrusts out his copulative organs. Proper orientation to the longitudinal axis of the female is accomplished immediately by the male's holding fast on both sides to the sharp edges of the tergites. The position rear end to rear end is achieved after more or less hasty, occasionally (especially in the case of Phausis) repeated moving about on the female with lightning-quick turns, the male, with violent movements of the antennae, apparently remaining in fairly

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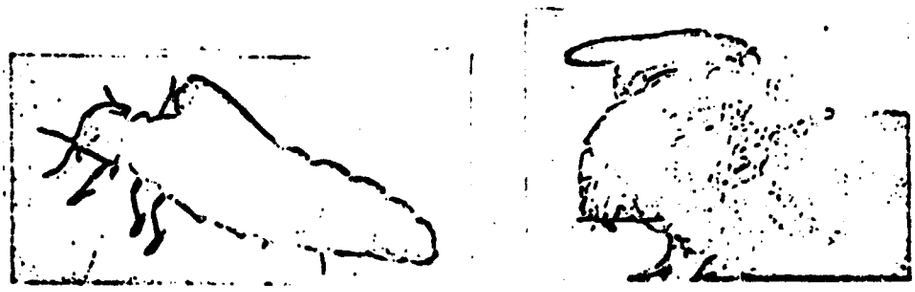

62 63

Figure 62. At the touch of the male after the flight, the female gives up the glowing posture; orientation of the male to the female (Lampyris pair).

Figure 63. After proper orientation the male "hunts" for the female genital opening, moving backward and with copulative organs protruded.

long contact with the head or with the tip of the abdomen of the female (Figure 62). Upon correct orientation to the female the pincer-like parameres open and close, with simultaneous exploratory movements of the entire copulative organs (cf. Figure 100). In response to this tactile stimulus the female raises the tip of the abdomen slightly. (This may also be induced experimentally with a soft brush.) The Lampyris male, after making contact with the fore end of the 1-1.5 times larger female, moves relatively slowly back along the female's back, continuing to "hunt" with the copulative organs in the intersegmental membranes of the tergites, pleura, and sternites (Figure 63). These experiments usually last as long in Phausis as the copulation itself, while Lampyris usually achieves coupling within a few seconds. During coition (Fig. 64a,b) (in Phausis about 15 minutes, in Lampyris 20-90) the female's light intensity quickly drops as a rule to a glimmer or the luminescence disappears entirely. In cases where the luminescence continues with undiminished intensity for a while after coupling is achieved, other males (according to field observations) gather depending on the population conditions, and in a wildly agitated struggling tangle around the female they try with lowered prothorax to push away the already copulating male. In this crowding the pair get into all possible positions. During coition the female, except for slight movements of the abdomen, ordinarily remains completely still; the male moves the antennae at lower frequency than during the orientation and coupling attempts. The Lampyris male often appears to fall into a copulation akinesis. Lampyris is hardly disturbed in copulative attempts or during actual coition by mild photic

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64a 64b

Figure 64. Copulation position in Lampyris (a) and Phausis (b).

and tactile stimuli. Phausis males immediately separate from the female, flee or play dead. The fact that light stimuli (not above 200-400 lx) do not disturb copulation in Lampyris is in harmony with the fact that Lampyris, in contrast to Phausis, copulates in diffuse daylight. No changes are observable in the copulation behavior under these conditions. Phausis males are ready to copulate 1 to 2 hours before and after the normal period of activity. After copulation the female crawls away and hides, but the male does not always do so, for at least in laboratory experiments copulation can in both species be repeated several times (with the same or other females). Thus I observed two Lampyris males that after a 10-15 minute pause each time performed 4 and 3 copulations respectively of normal duration (20, 25, 36, 60 and 48, 40, 50 minutes). This repetition of copulation within one activity phase or within the brief imaginal period, often observed (in the laboratory), is not characteristic for short-lived insects. Occasionally after separation the Lampyris male remains on the back of the female in the copulation position but without further attempts at copulation and is carried around by the female. I was not able to observe such behavior in Phausis.

d) Perversions

Among males of both species attempts at copulation not infrequently occur (observed both in the field and in the laboratory) (Figure 65). The males show the same behavior as toward females: mounting the back of a male, hasty, uncontrolled movements, vibration, searching for the genital opening with protruded copulative organs, orientation on the male. Copulation attempts between males were observed of over an hour's duration. While most of the attempts at copulation do

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Figure 65. Attempt of two Lampyris males to copulate.

not lead to union, in one case I observed an actual copulation of two Lampyris males, where the penis with the parameres had penetrated between the sexual appendages of the other male and was anchored fast there. The intensity of sexual excitement seems to be in no way diminished in homosexual copulation attempts. The "attacked" male usually runs about constantly but without being able to shake off the perverted one. -- That this perversion has little connection with luminescence is clearly shown by Lampyris males, which do not luminesce and in whom nevertheless homosexual relations occur oftener than in the luminescing Phausis males, often proving a hindrance in decoy experiments. Among the males of American lampyridae copulation attempts have been observed by McDermott [86] in Photinus marginellus and Pyractomena borealis and by Buck [21] in Photinus pyralis; these are forms with not very marked sexual dimorphism (wings and functioning luminous organs in both sexes), in which homosexual activity is easier to explain than in our native species with extreme sexual dimorphism.

I found an inexplicable peculiarity in Phausis females. In one night I found 17 females of that species at an uncommon altitude for Phausis females -- 30-50 cm above the ground -- glowing in perfect glowing posture. Under the usual conditions of captivity 12 of these females died overnight, and the rest during the day. Subsequent examination showed that these noticeably flattened females had not a single egg left in their ovaries. This is the only case in which I have found complete sexual appetency behavior of the females after egg-laying.

2. Reaction to Ordinary Artificial Light

The older authors (Avesbury [cited according to McDermott, 84], Bugnion [26], Morley [94], Newport [95], Olivier [96], Vogel [131]) report positive phototaxis of Lampyris males to lamplight. Since no information is available as to the intensity of the lamps and since I never succeeded in catching the (non-luminescing) Lampyris males I needed with spotlights, as I first tried to do, it is to be assumed that those observations involved very weak sources of light no long-

er in use at the present time. When I was working in the open with an almost burned-out pocket flashlight Lampyris males did occasionally fly up to me, but so rarely that female luminous decoys at any rate were more effective. Nothing was known of positive phototaxis in Phausis males, and I could not attract them, either, in the open by using pocket flashlights of varying strength. Bugnion probably observed best when he stated that Lampyris males come near (!) lamps; presumably just not near enough to get into the light of the lamp, which is too strong for them [see Note]. The experiments of McDermott [84, 87], Mast [82], and Buck [19,21] concerning the signal system of American lampyridae were carried out with matches, candles, pocket flashlights and the like, without imitation of the female's luminous field. In nearly all cases, of course, the males showed definite positive phototactic reactions when the flashing was done according to certain flash patterns.

[Note] Cand.rer.nat. W. Hüther informs me that in catching insects at night with a carbide lamp he has caught Lampyris males, which to be sure did not fly directly to the source of light, but flew around the lamp at a certain distance.

My observations on the imagines (males and females) of our two native species of lampyridae showed over and over that they reacted with both positive and negative phototaxis toward artificial light.

a) Phototaxis

Positive phototaxis is clearly proved for male imagines at a definite intensity by the possibility of attracting the males of both species by the female light or by artificial light (cf. Chapter D II 1). Lampyris females that were in the petri dishes in various decoy experiments also ran toward the light decoys when they happened to get near them. In Phausis females no similar behavior was observed.

With too great intensity of the decoy lights (in comparison to the female light) the activity of the males declined or stopped completely. In the experiments concerning the excitative effect of decoys of varying brightness an intensity-dependent behavior was also found. If the overhead lighting of the room (about 500 lx) was switched on during the active period, the imagines (males and females of both species) crawled away and hid. The males immediately stopped glowing, dropped to the floor, and, with eyes covered with the prothorax, went in search of a hiding place; the females reacted somewhat more slowly (especially the Phausis females), but also ceased to glow, gave up their glowing posture, and crawled away to hide. After a few minutes of darkness their complete sexual appetency behavior was restored. Weak light did not disturb the in-

sects in their activity. They thus appeared to react positively or negatively pototactically depending on the intensity of the light. This question will be studied below for the males of both species. Gradually increasing and decreasing (measurable) changes in intensity of the lighting during the insects' activity period were tried. Since the movement phase necessary for these experiments lasts in the females of the two species only from the time of leaving the hiding places to the assumption of the glowing posture, and so is very brief, the change from negative to positive phototaxis was investigated only for Lampyris females and rather crudely. It took place between 200 and 500 lx. That the glowing females attract each other mutually was never to be observed. (See Table 15.)

Results (Table 15): With gradually decreasing intensity the behavior took place in reverse sequence. The change from positive to negative phototaxis is not sharp (sharpest in Phausis males), since not all individuals react with equal sensitivity to light. To arbitrarily selected intensities the insects reacted as shown in the Table, even in the case of change from 2000 to 20 lx; within 5-7 minutes the males were active and positively phototactic, the females (more sluggish in general than the males) after about 15-20 minutes.

Negative phototaxis was exhibited by male and female imagines when exposed (at 500 lx) to green, yellow, red, and blue light, red light having a less powerful effect, especially on Phausis males. While they assumed the characteristic posture for great light intensity, they did not crawl away to their hiding places until the subsequent illumination with normal light (500 lx).

b) Scototaxis

The same experimental arrangement described for the larvae was also used for the imagines and is illustrated in the same way (Figures 66a,b). Here, however, the petri dish was lighted to 1000 lx. The experiments were carried out with 10 insects each during the nightly activity phase.

The males of both species showed definite scototaxis. In Figures 66a,b A the males of the two species were all at the dark wall after 10 minutes (•). The positions (•) in Fig. 66a B were helt by Lampyris after 10 minutes, by Phausis (Fig. 66b B) after 15 minutes. Comparison of the path diagrams of Fig. 66a B with those of 66b B shows that Lampyris males react more quickly and exactly than Phausis males. The males assumed at the dark wall the well-known posture assumed under too powerful light (prothorax as shade, head retracted). They seldom left the dark wall (especially Lampyris), and if

Table 15.

Intensity of a Directed* Light Beam	Reaction (+ Positively, - Negatively Phototactic)			
	Lampyris Males	Phausis Males	Lampyris Females	Phausis Females
10 lx	all +, remain inactive at source of light	+	glowing in normal glowing posture	glowing in normal glowing posture
20 lx	as above	+	as above	as above
40 lx	as above	+	as above, but some not glowing	as above
60 lx	as above	+, but decreased activity, no attempts to fly	as above	as above
80 lx	as above	indifferent, completely motionless; head retracted, prothorax bowed	give up glowing posture, but not yet in hiding place	as above
100 lx	as above	25% definite: digging movements on the spot with legs & prothorax	as above	abdomen brought into normal position; remain on the spot, glowing
150 lx	as above, reaction slower	as above	as above	as above
200 lx	about 50% +, the rest - or indifferent. Reaction very sluggish	as above	some in hiding place	as above, some running about
300 lx	as above	as above	as above	as above, emitted light becomes weaker
500 lx	less than 50% +; many go away from the beam at some distance from the source of light	as above	all in hiding place	as above, but look for hiding place

*The females in glowing posture were subjected to diffuse overhead lighting in the intensities shown.

Table 15 (continued).

Intensity of a Directed Light Beam	Reaction (+ Positively, - Negatively Phototactic)			
	Lampyris Males	Phausis Males	Lampyris Females	Phausis Females
700 lx	less than 15% +, the rest -	50% as above	no change	all in hiding place
1000 lx	all -	70% as above, more rapid movement	no change	as above
1500 lx	as above	all as above, but more violent movement	no change	as above
2000 lx	as above	as above	no change	as above

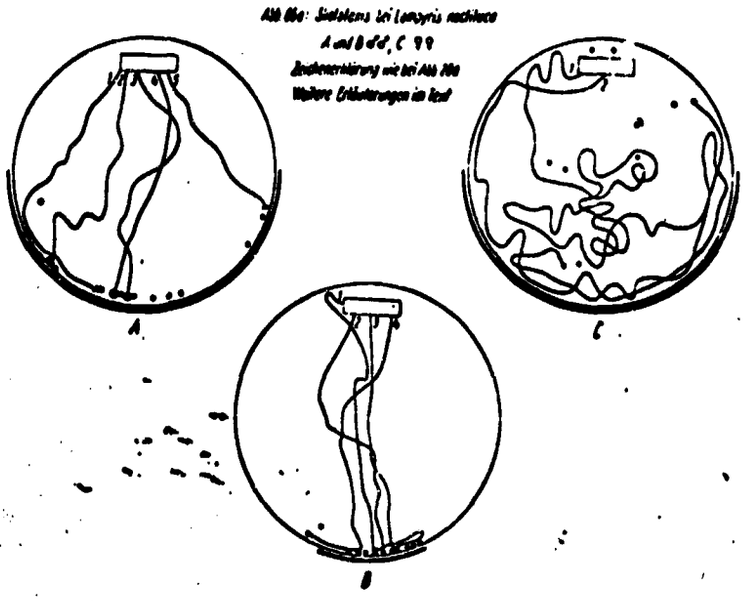


Figure 66a. Scototaxis in Lampyris noctiluca. A and B, males; C, females. Meaning of symbols as in Figure 20a; further explanations in the text.

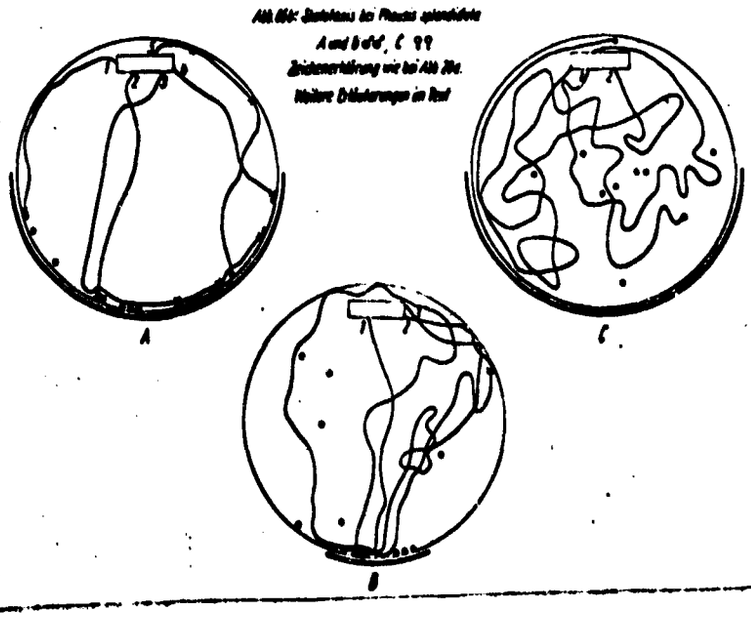


Figure 66b. Scototaxis in Phausis splendidula. A and B, males; C, females. Meaning of symbols as in Figure 20a; further explanations in the text.

they did they always went back to it (e.g. Figure 66b B 3).

The females of the two species showed no scototactic reaction or no definite one. The behavior of the female in Figure 66a C 2 might suggest that when she got very close to the dark wall she did perceive it. The paths of the other females (for clarity only a total of two are shown here) are like that of no. 1. The location of the individuals of the two species after 30 minutes allow of no positive statements either.

c) Experimental Work on the Day-Night Rhythm of Imagines

The question of what determines the day-night rhythm is generally interesting in the case of luminescent animals, and is especially important if we wish to appraise their behavior under largely normal conditions.

There are two opinions as to the relation of the day-night activity rhythm to the luminescence of the firefly imagines: 1. that this rhythm is a periodic phenomenon largely independent of immediate environmental factors (Mast [82]), and 2. that the periodicity can be modified by environmental conditions (Allard [cited according to Harvey, 55], Buck [20], Perkins [101], Rau [109], Newport [95]).

That the temperature variation normally occurring in summer plays no part in the appearance of the imagines has been shown in Table 14. The same table also shows that with natural variations of the intensity of daylight (with cloudiness, storms, earlier onset of darkness with the advancing season) the activity begins earlier (repeatedly observed in both males and females!!). On the other hand full moon, street lighting, and the like cause no delays in the period of activity or inhibitions of activity such as Czepa [31] and others report. In this connection I should like to mention again the summary (Table 15) which shows that the imagines remain active at low light intensities. Checks at the habitats show that even modern neon street lighting hardly reaches an intensity of more than 15-20 lx, and thus does not reach the effective inhibiting range.

The series of experiments (I to V) on this problem were carried out with our native lampyridae (the other authors' results were obtained chiefly with the American lampyrid Photinus pyralis), at a constant room temperature of 21° C (max. ±2°C) and at 100% relative atmospheric humidity (III-V predominantly with Lampyris females, since the males were urgently needed for decoy experiments). The insects were kept for at least 24 hours before the beginning of the experiment at normal undisturbed day-night rhythm in the experimental vessel (petri

dish 30 cm in diameter and with the most natural possible bottom). Observations were taken hourly and in many cases, e.g. at the beginning or end of the normal activity phase, quarter-hourly or half-hourly. The series were repeated several times and were checked over a period of 24 to 72 hours. (The short lifetime of the imago must be borne in mind, and also the fact that in most cases it will already have lived several days in the open.) The number of experimental animals was never less than ten.

Experiments on the normal day-night rhythm. (1)

First we were interested in the effect of artificial changes in intensity within the natural activity rhythm.

a) Two petri dishes (A and B) were both occupied by males and females of both species. In B were control subjects exposed to the normal daily rhythm (but with constant humidity and temperature). A was lighted from 17:00 on with 500 lx of diffuse lamplight (= average daytime brightness of the laboratory). At that time all the insects were hidden under leaves and the like, completely inactive. The control subjects began to glow at 20:50, while the animals in A remained in their hiding places. At 20:30 [sic] A was darkened; after 5-10 minutes all the males were active, and after 15-20 minutes the females, always more sluggish, showed the complete sexual appetency behavior (glowing on an exposed spot in the glowing posture). After 30 minutes' darkness A was again lighted with the same intensity; within 10 minutes all the males had disappeared into hiding places; the females stayed in glowing posture for a little while, with gradually decreasing intensity of luminescence, but after 20 minutes were in their hiding places. This change was repeated toward midnight with the same results, except that the insects became active noticeably more slowly after the darkening (at 23:45). At about the same time the control insects ceased their activity (the males earlier than the females).

b) Experimental conditions as in a). The insects (A) were subjected continuously from 17:00 to 24:00 to 500 lx. They all remained inactive and did not glow. From 24:00 on darkness was provided; after 3 minutes all were active, and after 15 minutes all the females exhibited complete appetency behavior (the first after only 6 minutes). They glowed until about 2:30 with undiminished intensity and shortly after 3:00 gradually stopped glowing and crawled away to hide, -- after about 2 1/2 to 3 hours! The control subjects (B) were active toward 21:00 and gradually ceased their activity about 23:30.

Constant Darkness (II). With constant darkness after preceding normal day-night rhythm the insects -- at whatever time of day -- left their hiding places immediately or after 1 to 2 hours, but did not glow or glowed only with a faint glimmer (in the case of the females mainly with the larval luminous organs); the females sought out exposed places, but left them again or stayed there often for hours without glowing, either in the normal walking posture or in the glowing posture. About 2 to 3 hours before the controls' usual time the insects became maximally active and showed normal sexual appetency behavior, which died out before midnight. During the remaining hours of the night they behaved as described above, usually not looking for hiding places but showing little or no activity.

Although the normal strict rhythm of activity and luminescence seems somewhat disturbed by constant darkness, still the recurring 24-hour rhythm is essentially maintained, but appears somewhat prolonged in its active phase through earlier beginning.

Constant Light (500 lx) (III). Even with constant illumination for several days the insects (here only Lampyris and Phausis females were tested) remained motionless, not glowing, for several hours in the same posture (in one case for 28 hours).

Day-Night Reversal (IV). When the vessels were darkened at a normal daytime hour (e.g. 8:00 a.m.) after several days of constant brightness, the insects (Lampyris and Phausis females) within 10-15 minutes showed complete sexual appetency behavior for about 3 hours. This observation prompted me to create periodic reversed day-night conditions by illumination at night (from 18:00 to 8:00 with 500 lx) and darkening in the daytime (from 8:00 to 18:00). Even in the first experiment, which followed the constant illumination (III), they behaved as in the normal day-night rhythm (i.e. active in the dark, inactive under illumination), maintaining the 2-3-hour period of activity and luminescence.

If this experiment follows a normal day-night rhythm, the insects need 12 to 24 hours to convert, since day is followed by "day" or night by "night + day."

Six-Hour Cycle (V). This shortened cycle was arranged under the lighting conditions used in the day-night reversal (only with Lampyris females). A nocturnal constant illumination (from 18:00 to 10:00) was followed by the first six-hour dark phase, then the lighted phase of the same length, and so on. Result: completely normal appetency behavior, regardless

of whether the dark period fell during normal daytime or night; the 2 to 3-hour period of activity and luminescence was maintained. After this phase the females were not luminescent, -- a few at first in the glowing posture without glowing, others in the hiding place and inactive, even when the activity phase occurring under normal conditions coincided with the period of illumination (e.g. during the illumination period from 16:00 to 22:00).

Lastly I have one series of experiments to report which I carried out with blind Lampyris females. The eyes of the females were painted under narcosis with a shellac mixed with lampblack, and this was checked under the microscope for opacity. The experiments were begun 36 hours after the treatment.

a) Normal day-night rhythm: The females began with normal appetency behavior about 1 to 2 hours before the control subjects, glowed until toward midnight, and then and during the daytime sought out hiding-places, which were usually not very well protected against light. Compare to this the behavior of normal insects in constant darkness (II).

b) Constant darkness: No influence on the females; behavior as in a).

c) Constant light: Behavior as in a).

d) Day-night reversal: Behavior as in a).

3. Sexual Dimorphism

(morphological comparison of the eyes of males and females of the two species)

In spite of the constantly recurring references in the literature to dimorphism in the development of the eyes of males and females of the lampyridae (Figure 67), there have been no morphological or other comparative studies of it (not even for the American lampyridae). Only Leinemann [71] gives the number of facets comparatively for the sexes of the two species (Lampyris: males 2600, females 700; Phausis: males 2500, females 300). Exner [39] studied only the Phausis eye, and specifically the morphology and the physical characteristics of the dioptric apparatus.

It is intended here mainly to compare the eyes of the two species and of the sexes with each other, in order to discover the relationships to the mode of biological function.

a) Morphological Structure, Point of Intersection of the Optical Axes, Number of Facets, Field of Vision

Morphological Structure. -- The cross sections (Figures 68 and 69) [see Note] were prepared essentially in accordance with the practices described in detail by del Portillo [103].

[Note] After the evaluation of the sections the slide box unfortunately was dropped on the floor, so that the sections became unusable, especially those of the longitudinal sections of the male eyes. For that reason the microphotographs that were to have been taken later are lacking.

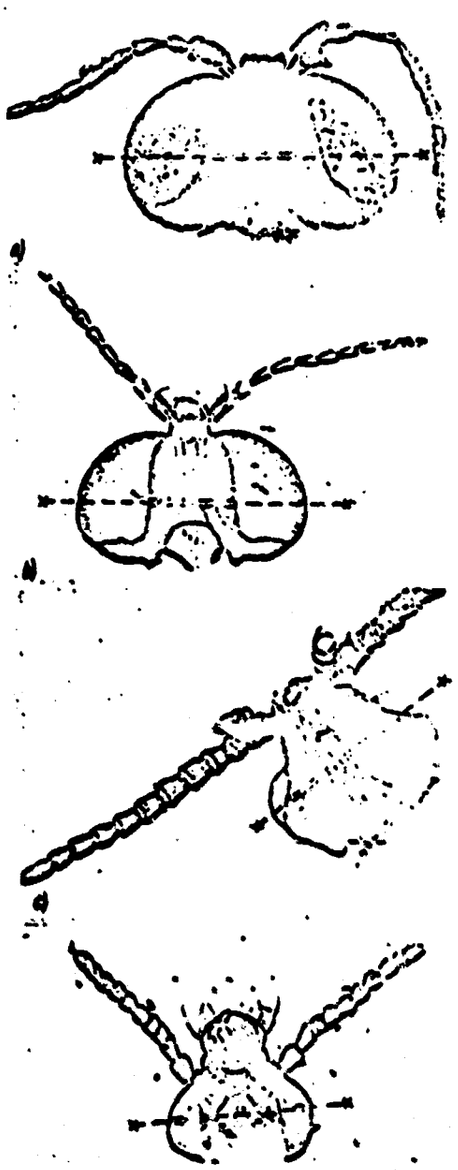
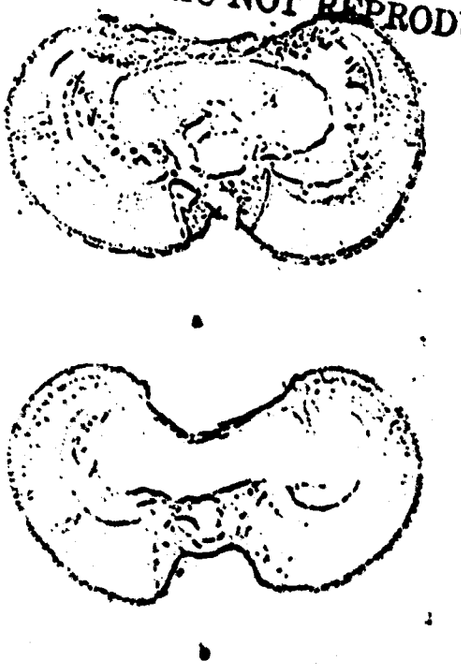


Figure 67 (left). Eyes of both sexes and both species, overall view from beneath. a) Lampyris male; b) Phausis male; c) Lampyris female; d) Phausis female. x---x plane of section of Figures 68-69.

Figure 68 (below,right). Dorsoventral section through the male eyes in the plane of greatest ventral extension of the eyes (marked x---x in Figure 67a,b). a) Lampyris male; b) Phausis male.



The illustrations show the basic similarity of the male eyes and of the female eyes of the two species. In function the eyes are typical superposition eyes, but in their internal

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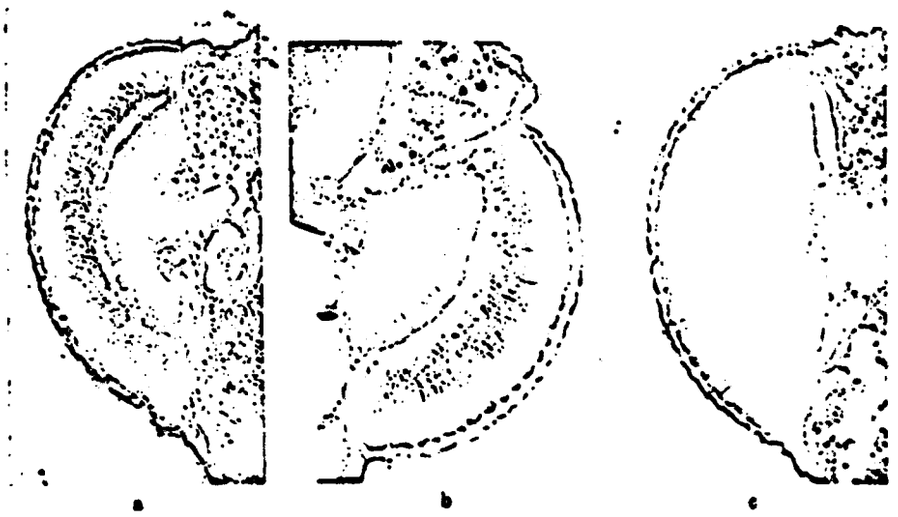

Figure 69,a-d. Sections through the female eyes of the two species.
a) Lampyris ♀ , dorsoventral section.
b) Lampyris ♀ , horizontal section.
c) Phausis ♀ , dorsoventral section.
d) Phausis ♀ , horizontal section.
Plane of section of the dorsoventral sections in the greatest ventral-dorsal extension (marked x---x in Figure 67c,d). Plane of section of the horizontal sections in the greatest rostral-caudal extension of the eyes (approximately corresponding to the optical section in Fig. 67c,d).

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and external morphological structure they have characteristic peculiarities.

The Male Eyes. —

Dorsoventral cut (in the plane of greatest ventral extension of the eye, marked x---x in Figure 67a,c):

External and internal asymmetrical structure, relatively great extension toward the ventral median, orientation of the facets downward (about 2/3), non-uniform curvature of the surface of the eye (dorsal third showing greater curvature) (Figure 68a,b), increasing lengthwise development of the visual elements toward the ventral direction (e.g. cornea and crystalline cone ventral in Lampyris 110-115 μ, in Phausis 95-100 μ, dorsal in Lampyris 55, in Phausis 45-50 μ) (Figure 70).

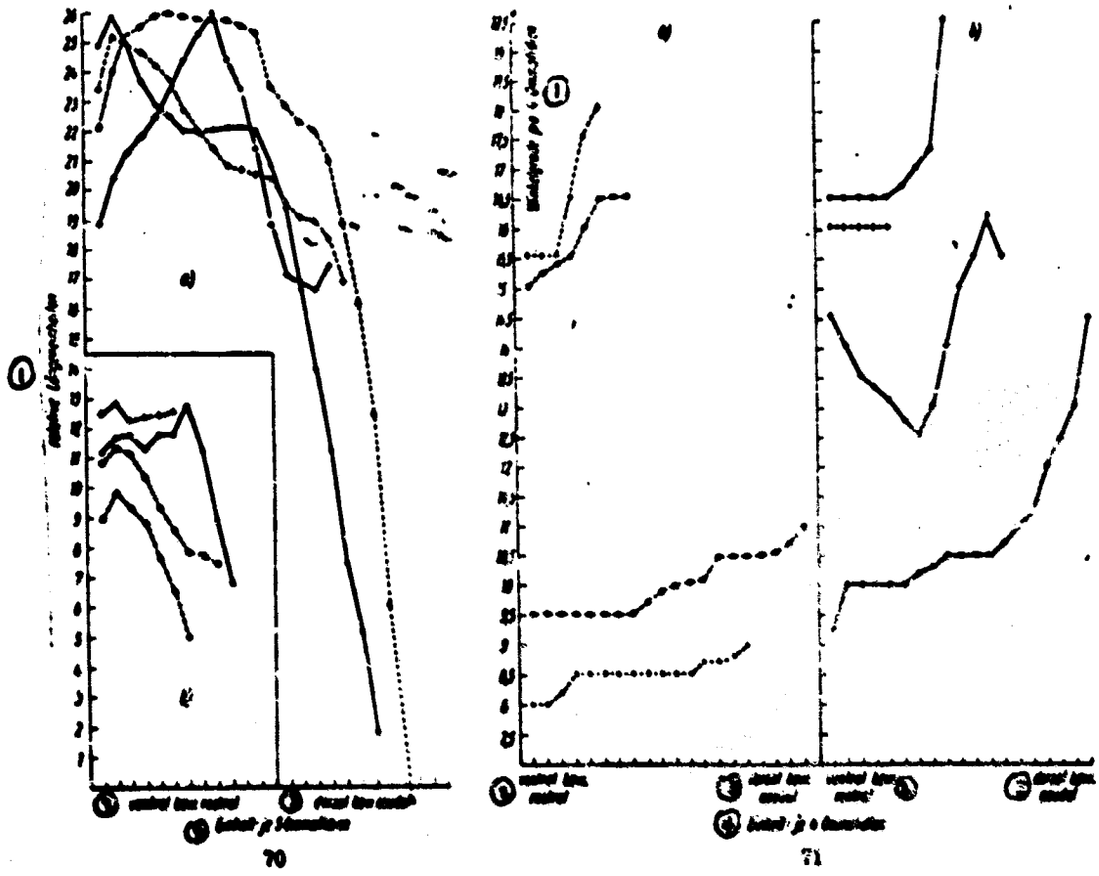


Figure 70. Length of the optical axes. a) Lampyris and Phausis males; b) Lampyris and Phausis females. ····· Lampyris from ventral to dorsal rim of the eye; +····+ Lampyris from rostral to caudal rim of the eye; ·-·-· Phausis from ventral to dorsal rim of the eye; +—+—+ Phausis from rostral to caudal rim of the eye. 1) Relative units of length; 2) ventral and rostral respectively; 3) dorsal and caudal respectively; 4) unit: 5 ommatidia.

Figure 71. Angles of ommatidia from ventral to dorsal and from rostral to caudal respectively in the planes of section shown in Figures 67 and 68. a) Lampyris males (below) and females (above); b) Phausis males (below) and females (above). Symbols as in Figure 70; legends as in Figure 70 except: 1) degrees of angle per 4 ommatidia; 4) unit: 4 ommatidia.

increasing angle of aperture of the ommatidia from ventral to dorsal (Figure 71).

Horisontal section (in the plane of greatest rostral-caudal extension of the eye, approximately corresponding to

the optical section in Figure 67a,b).

Eyes directed forward, almost radial, hemispherical external structure, though the internal structure does not entirely correspond to the external: in Lampyris the eyes are oriented toward the front (smaller angles of optical axes, greater radii = relatively slighter curvature), while the eyes of Phausis males are best developed laterally (Fig. 70).

The Female Eyes. —

Eyes of both species oriented somewhat ventrad and forward, and externally of radially symmetrical structure in the horizontal and dorsoventral directions (Figure 69a,d); in Phausis the internal structure corresponds to the external, radially symmetrical structure in the horizontal section (Fig. 69d and 73b), but not in the dorsoventral direction (Figures 69c and 73b). The eyes of Lampyris are developed internally in both directions asymmetrically to the external radial symmetry (Figures 69a,b, 73a).

Point of Intersection of the Optical Axes. —

The findings shown in Figures 72 and 73 were obtained by microscopic projection of the sectional preparations at about 1000-fold magnification. A focal ray was drawn from every fourth ommatidium.

The focal rays, regardless of asymmetrical structure, converge in the longitudinal and transverse directions in a single point in males and females of both species; i.e. they nowhere form focal areas. The focal point of all the optical axes is shifted upward and except in the Phausis female somewhat to the rear, and so does not coincide with the center of curvature. Since the corneae of the facets are equal in size, the angles must become greater toward the top and back (Figure 71) and the radii shorter (Figure 70). This has the result that the focal rays cannot be perpendicular to the surface of the eye in all cases. Surprisingly, they are perpendicular to the surface of the eye only in the front and ventral portions.

Number of Facets. —

The corneae and crystalline cones are fast grown together (pseudocone eyes), so that with fresh eyes that have been carefully cut out all the way to the edges the dioptric apparatus of the entire eye can be completely isolated from the sensory cells by brushing out. Eyes thus prepared were peripherally slit, imbedded in the usual way, and pressed between slide and cover glass. Such preparations were microprojected and the facets of ten eyes of each sex and species counted.

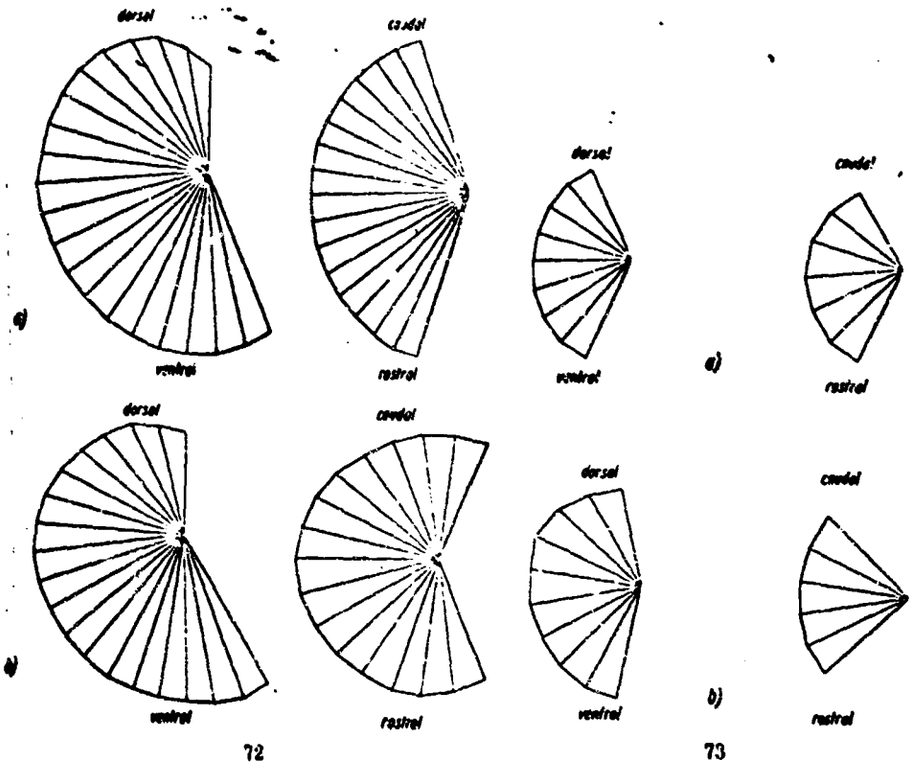


Figure 72. Point of intersection of the optical axes on the basis of dorsoventral (left) and horizontal sections (right): a) Lampyris males, b) Phausis males. Every fifth focal ray is drawn in.

Figure 73. Point of intersection of the optical axes on the basis of dorsoventral and horizontal sections: a) Lampyris females, b) Phausis females. Every fifth focal ray is drawn in.

The averages were 3412 facets for Lampyris males, 2750 for Phausis males, 605 for Lampyris females, and 375 for Phausis females. The eyes vary in size (especially great differences among Phausis females), so that among the males of the two species deviations from the average of up to 10% occur, among Lampyris females up to 15%, and among Phausis females up to 30%. The ratio of number of facets of the Lampyris male to the Phausis male is 1.24 : 1, between the Lampyris female and the Phausis female 1.61 : 1. The surface of the eye of the Lampyris male averages 5.64 times as great as that of his female, and in the Phausis male 7.34 times as great (the size of the facets is the same in both sexes -- about 25 μ in diameter).

Field of Vision

The field of vision was determined on the basis of the pseudopillae (cf. von Buddenbrock [25]). The microscopic sections were not usable for this purpose, since they were done vertically or horizontally, while the maximum extent of the facets does not always run exactly in those directions. Thus e.g. the surface of the eye of the males runs in a curved extension toward the ventral medial posterior direction, and therefore cannot be determined from longitudinal or transverse sections. Figures 74 and 75 show approximate average values for 10 specimens each, since the field of vision fluctuates somewhat with the size of the eye, — less in males than in females.

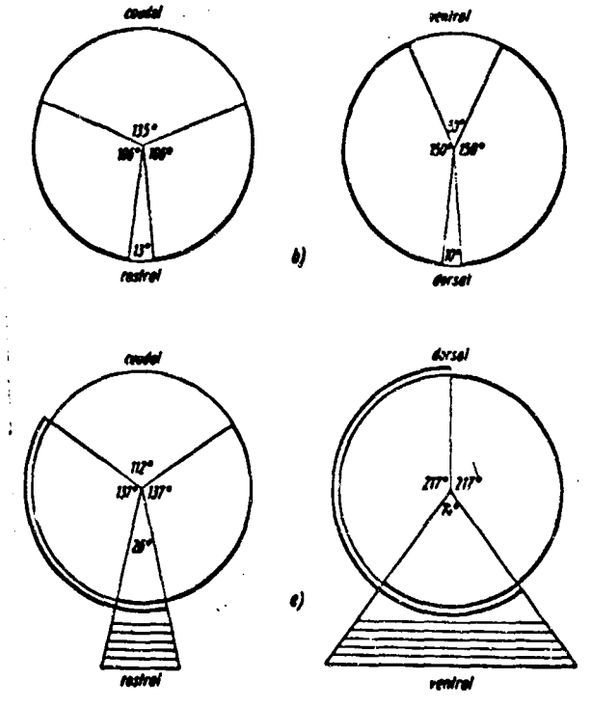


Figure 74. Field of vision of Lampyris males (a) and females (b). Right: from dorsal to ventral. Left: from rostral to caudal. Binocular field of vision shaded.

The field of vision of the males' eyes is usually 360° in the vertical (dorsoventral) direction, and up to 250° in the horizontal direction (from front to rear), with a gap in the field of vision at the back of the head (where it is joined to the thorax). The binocular field of vision in Phausis is up to 60° ventrally and up to 20° forward; in Lampyris it is 70–75° ventrally and up to 30° forward.

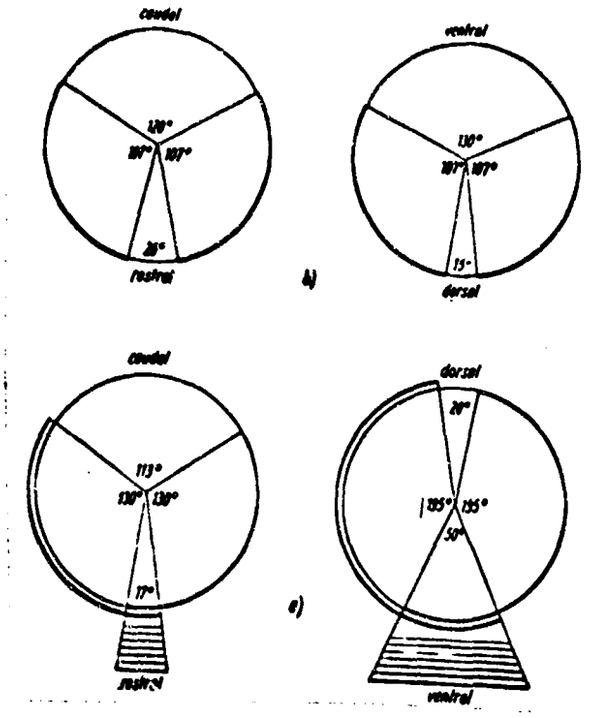


Figure 75. Field of vision of Phausis males (a) and females (b). For explanations see Figure 74.

b) Relationships Between Form and Function

As a rule typical superposition eyes are spherical in form, and the uniformly radial external structure is matched by a largely to almost absolutely uniform internal structure: uniformly developed ommatidia, forming equal angles with each other and undergoing no mutual shifts, being thus situated radially, perpendicular to the surface of the eye, with their optical axes intersecting almost in the same point; any specialization is practically ruled out.

The eyes of the females of the two species very closely approach such a structural type, but those of the males have undergone enormous modifications as compared to the normal morphological structural type of superposition eyes and become highly specialized organs which take up almost the entire surface of the head.

The most striking modification is the extension of the males' eyes toward the ventral and frontal median, by which

a considerable extension of the field of vision in all directions is achieved, but especially downward and forward. Two other facts besides the enlargement of the surface of the eye yield an extension of the field of vision: Increasing lengthening of the focal radii from dorsal to ventral and from back to front (Figure 70), and shift of the ommatidia out of the perpendicular to the surface (cf. point of intersection of the optical axes with the surface of the eye, Figure 72). By these two methods a different curvature of the surface of the eye is achieved, and thus indirectly an enlargement of the field of vision. These two methods also make it possible to orient the eye especially ventrad, but also forward, for by increasing or keeping constant the focal radii in the ventral or forward half of the eye on the one hand (Figure 70) and by shifting the point of intersection of the optical axes dorsad on the other (Figure 72) the facets are directed downward and forward.

The special enlargement of the field of vision toward the ventral and frontal median, in combination with a greater convexity, provides an especially large binocular field of vision downward and a smaller one to the front, serving mainly for distance localization and hardly inferior in development to those of predatory daytime insects (Laphria gibbosa 25°, Bembix rostrata 35°, Nepa cinerea 54°, Calopteryx splendens 88°, according to von Buddenbrock [24]). The high number of facets also favors localization.

These two striking specializations of a nocturnal insect (360° vision, binocular field of vision) are splendidly suited to facilitating recognition of the luminescing female, and together with the typical flight of the males (which see) make possible exact sighting of the female and accurate landing beside her.

An important question in connection with the active sexual behavior of the males is that of the light sensitivity of their eyes. Superposition eyes are generally characterized as light-catching organs, as the almost punctiform surface of the perceptive portion of the retina converges the twilight gathered upon a much greater surface of the dioptric system. In spite of the enormous deviation of the males' eyes from the typical radial structural design, the enlarged surface of the eye concentrates all the light in one point. A particularly rich tracheal ramification between the basal membrane and the lamina ganglionaris (especially in the 2/3 of the eye that is ventrally oriented) may be interpreted as a tracheal tapetum (unfortunately not visible in the microphotographs). This development of the tracheae is lacking in the females of both species. The sensitivity to light must be quite considerably increased by these two morphological peculiarities.

The resolving power or acuteness of vision is dependent on the number of facets in a given angle, and so is greater the smaller the angle that encloses the individual ommatidium. For the same size of eye, therefore, the narrow-angle eye is superior to the wide-angle eye, but the latter is more sensitive to light. Resolving power (or acuteness of vision) and sensitivity to light are thus tied to two conflicting conditions, for which a solution must be found if both are to be highly developed. The solution of the problem is accomplished in the Lampyris male eye in an excellent fashion: 1. The angles are reduced in the ventral and forward directions (to increase the acuteness of vision), and 2. the surface of the facets is kept large by extending the narrow-angled facets in the longitudinal dimension (no reduction in sensitivity to light). The acuteness of vision or resolving power of the male eye is in fact very pronounced, for it distinguishes fields of light formed in different ways in flying to the female (see decoy experiments). It is interesting in this connection that in the Phausis male eye the angular values in the posterior and upper half of the eye are much larger than in the Lampyris male eye, and must accordingly greatly reduce the acuteness of vision. We might attribute to this cause the incapacity of the Phausis male to distinguish different luminous fields and his consequent confusion of his females with those of Lampyris, if we do not intend to make fundamentally different (and phylogenetically more primitive) neural conditions responsible for that.

The non-uniform curvature of the cornea due to its deviation from the spherical form and the oblique position of the crystalline cones might impair the visual perception of shape, since distortions of the images formed are to be expected. The more exact (in comparison to Phausis males) orientation to dark surfaces (see scototaxis) in Lampyris males I evaluate as superior visual perception of form on the part of the Lampyris males. This is in agreement with the fact that they recognize the arrangement of the luminous surfaces in the luminous organs of the female as a species-isolating stimulus (see light decoy experiments).

Decoy experiments with monochromatic light (which see) and the phototaxis experiments with light of various colors (which see) tell in favor not only of the reception of these wave-lengths of visible light, but also, in the case of the selective choice of specific colored luminous decoys, of the color vision of the males' eyes.

The morphologically fine differentiation of the males' eyes (as compared to the almost primitive structure of the females' eyes) must be conceived of as an adaptation to the

sexual behavior, for through enlargement of the field of vision, a binocular field of vision, and light sensitivity and acuteness of vision of the eyes all the problems set are simultaneously and excellently solved.

II. Analysis of the "Female Pattern"

By the so-called "female pattern" is meant the inherited excitative mechanism of the male which selects specific key stimuli of the female and groups them into a single stimulative complex. As a basis for the analysis of this pattern we used the observations on the normal sexual behavior of the two species in the field and in the laboratory (Chapter D I). Besides optical components of the stimulus, olfactory and tactile components were also tested. But in order to be able to make pronouncements concerning the efficacy of the individual stimuli it was necessary to attempt to present the doubtful components of the stimulus to the male in as near isolated form as possible. The following investigations and experiments were carried out either in the natural biotope or, where specifically mentioned, in the laboratory under as nearly natural conditions as possible and during the nocturnal activity phase. The results of experiments with free-flying males can of course be only of a qualitative nature, but were nevertheless important as starting points for the series of experiments in the laboratory.

1. Excitatory Effect of the Female's Light

a) Experiments with Natural Female Light

To make it possible to answer the question of the much discussed function of the female light it was necessary to study the flight of the males with all non-optical stimuli (especially olfactory ones) excluded. I attempted to do this for both species in the field and in the laboratory as follows:

1. Isolation of the females in airtight and odor-proof weighing bottles with ground-in covers.

2. Indirect presentation of the female light by reflecting it upward perpendicularly by combinations of mirrors some 20 cm away from the hidden female. This method was combined with the first.

3. Offering artificial sources of light of about the same intensity as the female light. I used pocket flashlight bulbs whose spectrum extended over the whole visible range. The battery-powered series of bulbs gave off light without any sort of mask and without the pattern of luminous surface characteristic of females of a given species, as used later for light decoys (which see).

In all three cases the males flew straight and accurately to the isolated females, the "isolated" female light, and to the artificial light. The artificial light of the bulbs, however, was far from being as effective as the light of the other experimental arrangements. The second experimental arrangement, which does not exclude the finding of the female by olfactory means, nevertheless did not lead to a meeting of the two sexes, although they had come within about 20 cm of each other.

During these experiments I noticed that Phausis males also flew toward Lampyris female light, while Lampyris males paid no attention to the Phausis female light. I also observed this often in the field, where I found Phausis males beside Lampyris females, attempting for a long time (occasionally over an hour) unsuccessfully to copulate with the female of the other species. Later quantitative experiments (light decoys) confirmed this observation. I saw several Phausis males making intensive copulation attempts (with protruded, groping copulative organs and the behavior of the male in copulation mentioned above) on a Phausis male pupa.

Lastly an observation should be mentioned which also demonstrates the strong attraction by light: 10 cm from a copulating Lampyris pair a Lampyris female was placed, which soon glowed brightly. The male gave up the copulation posture, but still remained coupled with the female and dragged her with him to the glowing female, and mounted the latter, though still coupled with the non-glowing female.

These examples appear to exclude the possibility that there is a female odor in Phausis peculiar to the species. They also show for Lampyris a sexual effect of the female light, and in fact of light in general, independent of the female odor. Light is the sole precipitating stimulus for the approach flight of the males.

b) Physical Properties of the Light of the Two Species

Studies of the physical qualities of firefly light were a prerequisite to experiments with light decoys. Since all developmental stages of both species glow (except Lampyris males) and occur simultaneously in the insects' biotope during the swarming time of the males of both species, these investigations were carried out for all stages.

Spectral Range

Many authors have made statements as to the spectrum and color of firefly light. According to Murray (Experimental Researches on the Light and Luminous Matter of the Glowworm, etc., Glasgow, 177 pages) the light of Lampyris larvae is greenish; according to Lehmann ("Lampyris Prize Contest,"

Nova Acta Leop.Carol., Vol 30, 1862, pages 113-114) Lampyris light possesses red, yellow, and green components; according to de Bellesme [6] violet is lacking, red is abundantly and green maximally represented; Conroy [30] gives the only exact statements concerning our native fireflies, but unfortunately with regard to an English "glowworm" not further identified; from his descriptions it may have been a Lampyris noctiluca larva (cf. Table 16). Dubois [cited according to Harvey, 55] later reports that not only the spectra within the species but also in different developmental stages within the individual are different, and attributes this to differences in light intensity. He says that the Lampyris light is blue. Meissner [91] reports green light for the larva of Lampyris, while Knauer [68] reports bluish light for Lampyridae (without mentioning the name of the species. I have not been able to find statements concerning Phausis in the literature anywhere.

In the table [see next page] I give a chronological summary (partly according to Buck [22]) of the spectral range of fireflies studied down to the present (predominantly American species), the authors, and their methods of investigation.

The inaccurate, subjective, often contradictory statements by only the older authors concerning our native lampyridae are unusable for my purposes.

Technical: The insects' light was recorded with a spectroscope (Zeiss pupil spectroscope), attached by a connecting piece to the camera objective (Makro Kilar 1:3.5/40 mm; camera: Exakta Varex IIa), on the highly sensitive panchromatic Ilford Film (HPS 27/10° DIN). Conducting the relatively weak light of the insects through the many optical systems made exposure time up to 30 minutes necessary. — The long lighting time led to difficulties in taking the photographs connected with the peculiar nature of the animal subject. As has been mentioned, the larvae ordinarily glow only at completely unpredictable times and only when undisturbed. Getting spectra from them photographically was possible only during the periods immediately before molting, when they glowed continuously at uniform brightness with continuous slight mechanical stimulation. The same method could be used with the pupae. It was hardest to make the photographs of the female imagines, for first of all they glow only during their activity period, and then they stop at any disturbance (e.g. slight vibration; attempt to fix them in front of the slit of the spectroscope). The only way remaining was to get them in front of the spectroscope slit completely without disturbing them and during their glowing period (usually in the open). Any movement of the luminous organs away from the area of the slit then became a defective picture. To photograph the Phausis male light the males were decapitated or the isolated abdomen with the luminous organs slightly mashed and then fixed in front of the slit.

Photographing a wave-length scale over the spectrum being photographed made it unnecessary to close the slit as far as possible in order to determine the spectral range and identify the dark lines with the corresponding wave lengths. The slit remained opened to the maximum extent for all photographs, as did the shutter of the camera objective. For the rest, all photographic technical precautions were constantly maintained; the exposed films were all developed in the same tank under the same conditions (Ilford I D - 11 Fine Grain Developer, 14 minutes at 20° C).

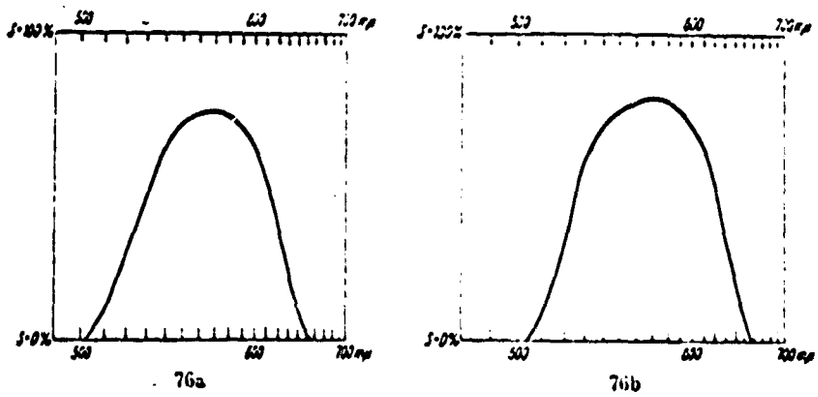
Table 16.

Species	Wave-length Range in mμ	Method	Author
Pholinus spec. (?) . . .	487—656	V	Young 1870
English glow-worm (Larve von *Lampyris*?)	518—656	V	Conroy 1882
Pyrophorus noctilucus			
Thorax	468—640	V	Langley & Very 1890
Abdomen	463—663	V	
Pholinus pyralis	525—640	P	Ives & Coblentz 1910
Pholinus pyralis	ca. 535—620	V	Mc Dermott 1910
Pholinus consanguineus .	ca. 550—615	V	Mc Dermott 1910
Pholuris pennsylvanica .	ca. 540—615	V	Mc Dermott 1910
Phengodes laticollis . . .	511—645	V	Mc Dermott 1912
Pholinus consanguineus .	525—640	P	Coblentz 1911, 1912
Pholuris pennsylvanica .	510—610	P	Coblentz 1911, 1912
Glow-worm (?)	529—586	P	Ramdas & Venkitesh-waran 1931
Glow-worm (?)	469—588	P	Brooks 1940
Pholinus xanthopholis catherinae ♂	535—640 (P)	520—655 (V)	max 585 Buck 1941
Same			max 580 Buck 1941
Pholinus pallens ♂. . . .	515—642,5 (P)	515—665 (V)	max 577,5 Buck 1941
Pholinus pallens ♀. . . .	520—645 (P)	512,5—655 (V)	max 577,5 Buck 1941
Pholinus synchronans ♂ .	515—645 (P)	520—655 (V)	max 585 Buck 1941
Pholinus variabilis ♂ . .	520—660 (P)	522,5—665 (V)	max 580 Buck 1941
Pholinus flavilimbatus ♂ .	—	527,5—620 (V)	— Buck 1941
Pholinus ceratus ♂ . . .	—	535—620 (V)	— Buck 1941
Pholinus evanescens ♂ . .	—	535—655 (V)	— Buck 1941
Pholinus gracilobus . . .	—	507,5—655 (V)	— Buck 1941
Diplotus uniscus	—	505—645 (V)	— Buck 1941
Diplotus montani	—	515—620 (V)	— Buck 1941
Diplotus semifuscus . . .	—	512,5—655 (V)	— Buck 1941
Pholuris jamaicensis ♂ . .	ca. 127,5 (P)	—	— Buck 1941
Pholuris jamaicensis ♀ . .	—	522,5—655 (V)	— Buck 1941
Pyrophorus glaziophthalmus			
Thorax	505—650 (P)	497,5—655 (V)	max 585 Buck 1941
Abdomen	540—645 (P)	515—655 (V)	max 595 Buck 1941
Phengodes spec.	—	510—590 (V)	— Buck 1941

V - visual method; P - photographic method of determining the spectral range; ? - no indication of species.

Spectroanalysis by the difficult photographic method was preferred because of its objectivity to subjective observation (the Purkinje effect, etc.). At the same time it permitted a comparative determination of the energy distribution of the spectral light on the basis of the darkening of the film.

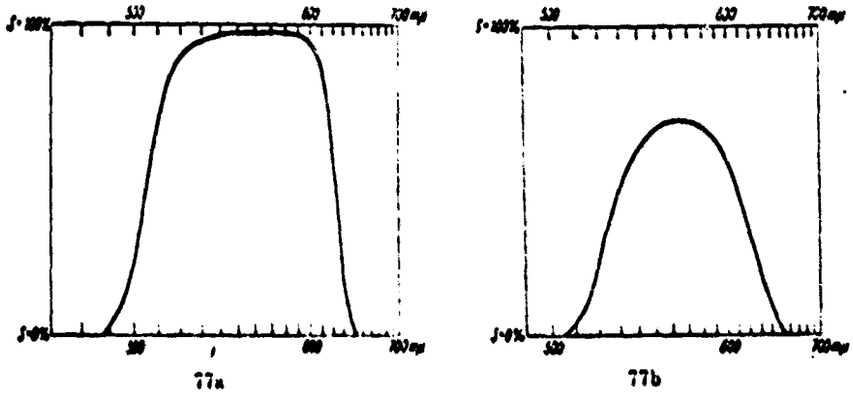
Results: The spectra of both species and in all stages of development lie in the same region of the visible spectrum as a continuous band from about 500 to 660 mμ. Details may be seen in the curves of the spectra in Figures 76-78. The results were confirmed on the basis of photographs of several



76a 76b

Figure 76 a. Spectral energy curve of the light emitted by the Lampyris larva. Exposure: 5 minutes. Ordinate: blackening of the emulsion side of the film (S); abscisse: wave length in mμ.

Figure 76 b. Spectral energy curve of the light emitted by the Phausis larva. Exposure time: 5 minutes. Notation as in Figure 76a.



77a 77b

Figure 77 a. Spectral energy curve of light emitted by the Lampyris female. Exposure: 5 minutes. Notation as in Figure 76a.

Figure 77 b. Spectral energy curve of light emitted by the Phausis female. Exposure: 5 minutes. Notation as in Figure 76a.

(at least 5) specimens for each stage of development.

Spectral Energy Distribution of the Light Emitted

The basis for determination of the energy distribution in the spectral band of the light emitted by the insects was the blackening of films obtained by the above method. The distribution of density of the blackenings in the spectral band corresponds to the light energy of the various wave lengths on the assumption of uniform color sensitivity of the film material, which is

guaranteed in the case of the panchromatic Ilford film. The density of blackening of the spectral band was measured photographically. [See Note.]

[Note] The measurements of density of blackening were made with a Zeiss rapid photometer with Steinheil recorder and photomultiplier I P 28. I cordially thank Dr. Eichhoff, of the Inorganic Institute of the University of Mainz for making the apparatus available, for making me acquainted with the technique, and for his readiness to help in manipulating the instruments.

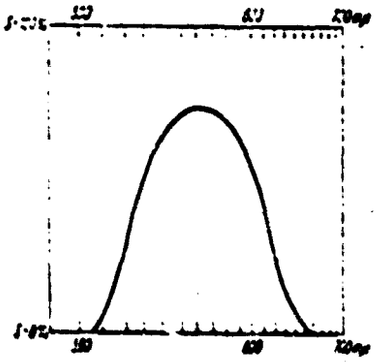


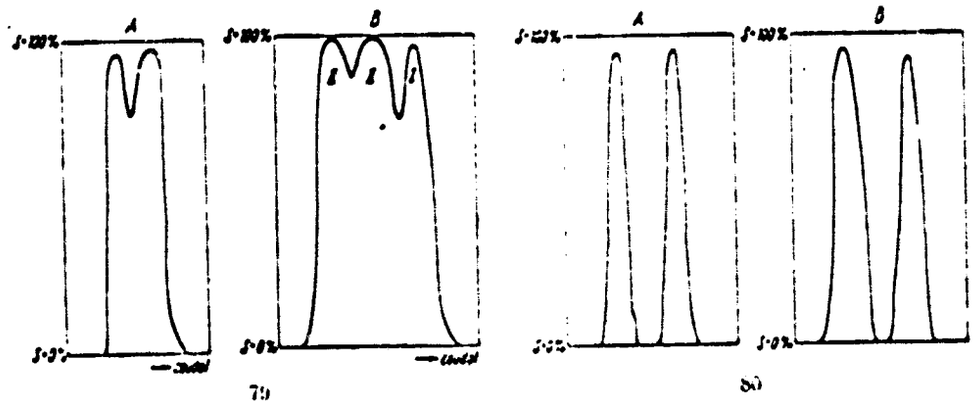
Figure 78. Spectral energy distribution of the light emitted by the Phausis male. Exposure time: 5 minutes. Notation as in Figure 76a.

Figures 76-78 show the direct measurement values of blackenings of the emulsion layer of the film. Since the width of the spectra lies in a range in which the emulsion is almost uniformly sensitive, the measured values largely correspond to the absolute data, i.e. the maximum of density of blackening is matched by an energy maximum of the insects, and the nearly symmetrical pattern of the curve is matched by a uniform (sharp) decrease in short-wave and long-wave components of the spectrum outside of this maximum value. The maxima for both species and all stages of development lie between 550 and 580 mμ, and thus in the yellow range.

Determination of Intensity

In order to compare the light intensity of the developmental stages of the two species, the luminous organs were macrophotographically recorded in their own light. To make possible short exposure times, Ilford HPS film was used for these photographs too. Prerequisites for comparable darkenings of the film and for later photoelectric registration were uniform distance from the objective lens, similar arrangements of apparatus, and similar conditions of photographic developing for all the photographs. The camera used was —as before— "Exacta" with the "MakroKilar" objective.

Figures 79-81 show that the maximum intensity exhibits not only very slightly diverging values for all developmental stages, but also that the intensity of individual parts of the luminous organs is equal. Nor can they confirm the



79 80

Figure 79. Density curves of a Lampyris larva (A) and a Lampyris female (B). I larval luminous organ of the imaginal luminous apparatus, II imaginal luminous plates. Distance from camera 12 cm, exposure 5 seconds. S = darkening of the negative. Abscissa: region of the luminous organs from thoracic to caudal.

Figure 80. Density curves of a larval luminous organ of Phausis. A from the dorsal, B from the ventral side; other explanations as for Figure 79.

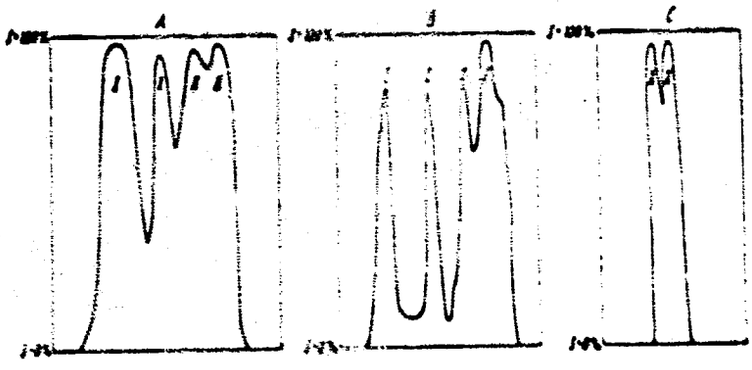


Figure 81. Density curves of the luminous organs of the Phausis female (A from the dorsal, B from the ventral side) and of the Phausis male (C). I larval luminous organs of the imaginal luminous apparatus (in the Phausis male not externally visible), II imaginal luminous plates; otherwise as in Figure 79.

assertions of Czepa [29], Macaire [76], Meissner [88], Verhoeff [126], and Weitlaner [129] that the entire body of the firefly glows (a support for the symbiosis theory!), for the photometer scanned the whole area surrounding the luminous organs and the body of the insect; results there: 0% density (in this connection cf. Figures 33a-e).

c) Decoy Experiments with Artificial Light

Knowledge of the physical properties of the female light as the principal key stimulus of the sexual behavior of the males formed the basis of the decoy experiments described below, which analyze the reaction of the males to variations of the most important artificially provided stimuli.

Method: Decoy experiments were done in the field only as a check on the laboratory experiments, because they lasted too long there and the results were consequently too scanty and could not be evaluated quantitatively, especially as the lifetime of the imagines is too short and experiments are possible only 2 to 3 hours a night, during the natural period of activity. Under laboratory conditions I was able by certain measures (cf. Chapter D I 2c) to extend the experimental time by about an hour without concern about abnormal influence. In the laboratory the decoy experiments were carried out at a room temperature of 20° C ± 2°, in a flight cage (1 x 1 x 1 m) the bottom of which consisted of a ground made to resemble that of the natural habitat of the insects (cf. C I) or in a petri dish (diameter 30 cm, height 10 cm) the bottom of which was lined with sand. Both containers always had about 95-100% relative humidity close to the ground.

The decoys consisted of cylindrical sleeves to one end of which the decoy mask to be investigated was fastened. (The abscissae of Figures 82-92 show the respective masks in actual size.) The height and width of the sleeves were such that they fitted closely over a pocket flashlight bulb (2.5 v, 0.5 amp), mounted on a foot that could be pressed down into the soft ground (for field and flying-cage experiments). This bulb lighted the decoy mask from beneath. Light filters, colored paper strips, frosted glass and the like could be put in front of the mask. To get a uniformly lighted mask surface, a frosted glass was always attached in front of the decoy mask. The lights were connected with each other and powered in the field by batteries, in the laboratory by an adjustable transformer. In both cases the light intensity could be modified by a resistance. The use of the same stock of bulbs and the same source of power for all series of decoy experiments provided from the outstart for a more or less uniform luminous energy. The number of decoys used simultaneously during an experiment was determined by the object of the particular experiment (abscissae of the figures). But in order that it would always be possible to check on the course of the experiment at a glance, not more than seven decoys were ever used. They were set up irregularly in the flight cage at more or less equal distances from each other. Around the petri dish they were set outside the dish at equal

distances of 2-3 cm, oriented toward the center of the dish and above the ground level. The petri dish arrangement was most successful and toward the last was used exclusively. The locations of the decoys were often changed during the experiments, in order to exclude any habituation phenomena. The males were thus basically subjected to multiple-choice tests. The males' eyes with their 360° vision allow of this method. The constant ratio of turning toward particular targets in the individual series and the behavior toward and at the decoys are evidence of a genuine spontaneous choice.

Comparison tests with glowing females could be used simultaneously with the decoy tests only in cases of special interest, since because of difficulties of procurement, because of the brief lifetime of the adult insects, and because of other difficulties repeatedly mentioned above, it is very tedious and time-consuming to get the females into a continuous state of luminescence and at the same time in a position visible to the males. For this purpose movable raised objects were put into the vessels with the females, on which they went into the constant glowing posture. For the comparison tests covered petri dishes were used exclusively, as they excluded any odor factor very conveniently, since the females when strictly separated from the males would glow outside the petri dish. Glowing females were constantly used, however, to regulate the light decoys and compare their intensity.

Evaluation of the experiments was done as follows: In the field and in the flight cage I counted the approaches by direct flight. In the petri dishes these approach flights occurred more rarely because of the short distance to the glass wall; here the males ran toward the decoys, as they did in the field when only short distances were involved. As a rule they ran in a straight line to the decoys, with vigorous antenna movements and other movements. In order to rule out chance, the decoys and the control females were set 2 to 3 cm above the ground. Climbing up the glass wall to the decoys showed the intentional approach quite unambiguously. Moreover the males usually spent a fairly long time near the decoys, went about in the immediate vicinity of the decoy with searching, rapid movements, and made butting movements with the head and prothorax against the glass wall in front of the light decoy, -- all symptoms that permitted a definite diagnosis of "approaches" of the males. The experiments could usually be performed in the dark, since the light of the decoys was bright enough. Otherwise a weak light from above was used, just sufficient for observation of the arrangement, and falling through a colored paper of the color least noticed by the males (for Lampyris blue, for Phausis green). These checks,

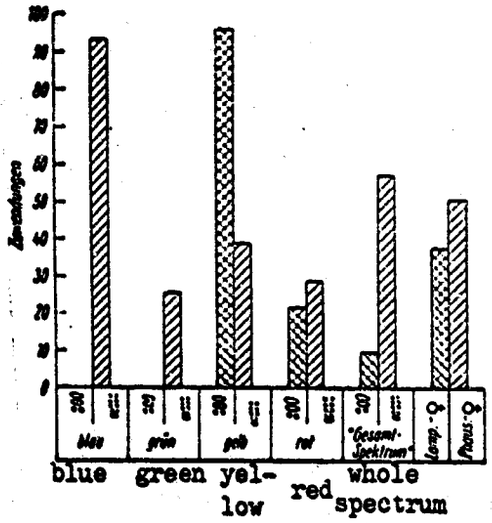


Figure 82. Reactions to light decoys.
Ordinate: number of approaches.
Abscissa: decoy masks, half actual size.

L (Lampyris noctiluca):
n (number of specimens) = 15;
N (number of reactions) = 166;

P (Phausis splendidula):
n = 30, N = 295.

Lampyris; *Phausis*.

lasting only a few seconds, did not disturb the males at all, even when they were running toward a decoy. The results of a series were regarded as confirmed only when counts of runs after certain intervals of time (e.g. after every 30 minutes) during the test period yielded no significant relative differences for the individual decoy patterns (total number of approaches on the ordinate of the graphs is the total count of often repeated experiments over a three-year period).

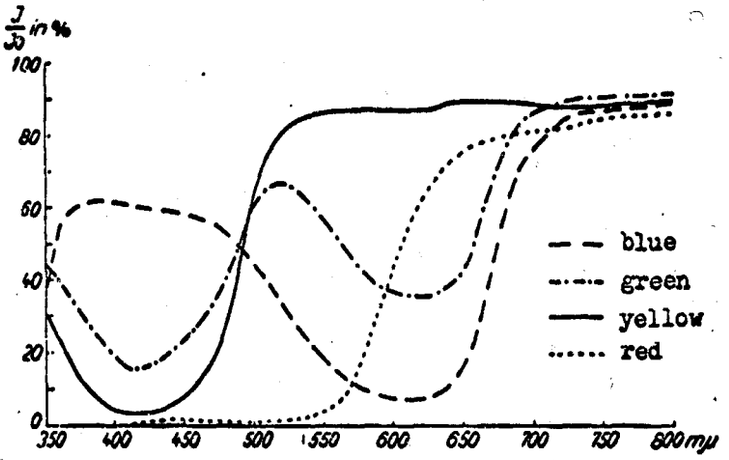
α) Color as the Distinguishing Feature

1. Reactions to the basic colors, blue, green, yellow, red, and to the whole spectrum of visible light (flashlight bulb light). The basic colors were produced by light passing through transparent colored paper [see Note] (Figure 82).

[Note] I am indebted for the measurements of the spectral curves of the colored papers to the Physics Institute of the Technical University of Brunswick through the kind offices of Prof.Dr. Schaller. They were done with a spectrophotometer Type Sb 500, "Unicam," no. 11768. The source of light was a tungsten lamp. Width of slit: 0.11 mm, I = intensity transmitted through the paper, I_0 = original intensity. Maximum scatter of the measured values 1.5. [For graphic representation, see the next page.]

2. Use of monochromatic filter colors [see Note] lying within the spectral range of the female light (Figure 83).

[Note] I thank the firm Jenaer Glaswerke Schott und Genossen here for the loan of the interference color filter used (manufacturing specifications: IL no. 629 416, 617 351, 631 048, 617 876, 135 417, 619 157, 608 806, 624 815 608 301, 620 472).



[See note on page 126.].

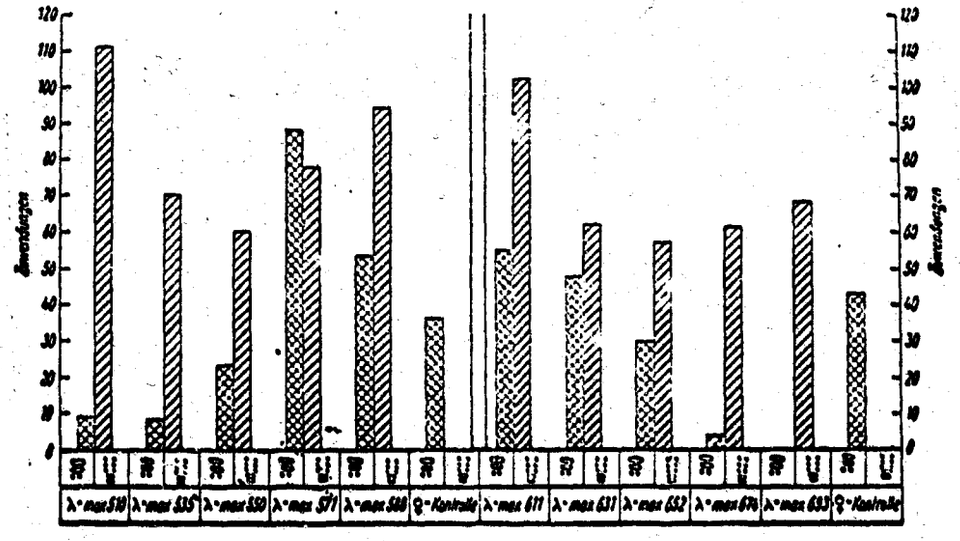


Figure 83. Light decoys with monochromatic filter colors. This experiment had to be carried out in two stages (I and II). Notation same as for Fig. 82. Last column in each half = female controls. L: $n_I = 15$; $N_I = 219$; $n_{II} = 15$; $N_{II} = 180$. P: $n_I = 30$; $N_I = 313$; $n_{II} = 30$; $N_{II} = 350$.

3. Comparison of a series of colored lights with the optimal excitatory colors shown in Figures 82 and 83 (Figure 84).

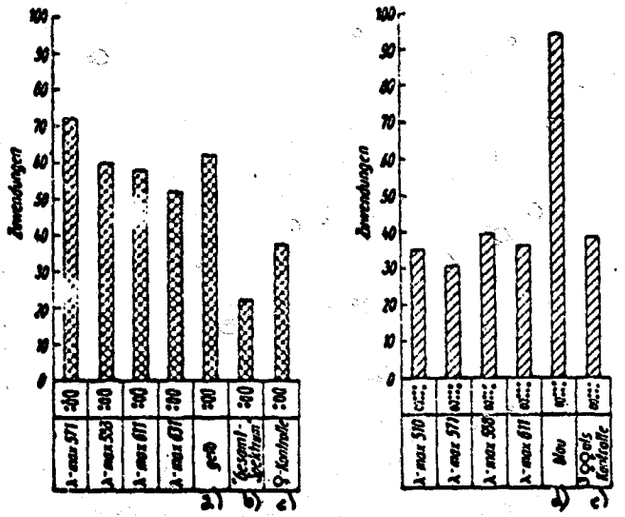


Figure 84. Light decoys: Comparison of the optimal excitatory colors. Left: Lampyris: n = 15, N = 363; right: Phausis: n = 30, N = 275. Vertical scale: approaches. a) yellow, b) whole spectrum, c) female controls, d) blue.

Lampyris pay little attention or none at all to the basic colors blue, green, and red, while they respond maximally to yellow. The more exact analysis with monochromatic color filters shows the same thing, and also shows that the energy maximum of the spectrum of light emitted by the female (around 570 mμ) coincides with the maximum number of approaches to artificial decoys that emit light of the same wave-lengths.

The same holds for Phausis males — maximum number of approaches when the wave-lengths are used in which the light emitted by the female is richest. On the other hand they differ very strikingly and unexpectedly from the Lampyris males on the following points: They react very well to all wave-lengths of visible light, and even have a second maximum in the blue light range that actually surpasses that in yellow light. It is a remarkable fact, however, that blue light is missing from the emission spectrum of all developmental stages, short-wave visible light being in fact represented there only at very low energy.

The comparison of the optimally excitatory colored lights (Figure 84) with genuine females demonstrates for both species that the corresponding monochromatic lights induce the approach flight of the males not only optimally, but "supernormally."

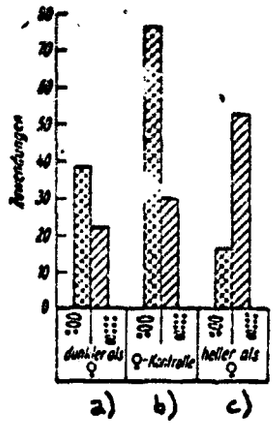


Figure 85. Light decoys: distinguishing characteristic brightness. Notation as in Figure 82.
L: n = 11, N = 130.
P: n = 30, N = 104.

a) darker than female
b) female controls
c) brighter than female

β) Brightness as the Distinguishing Feature

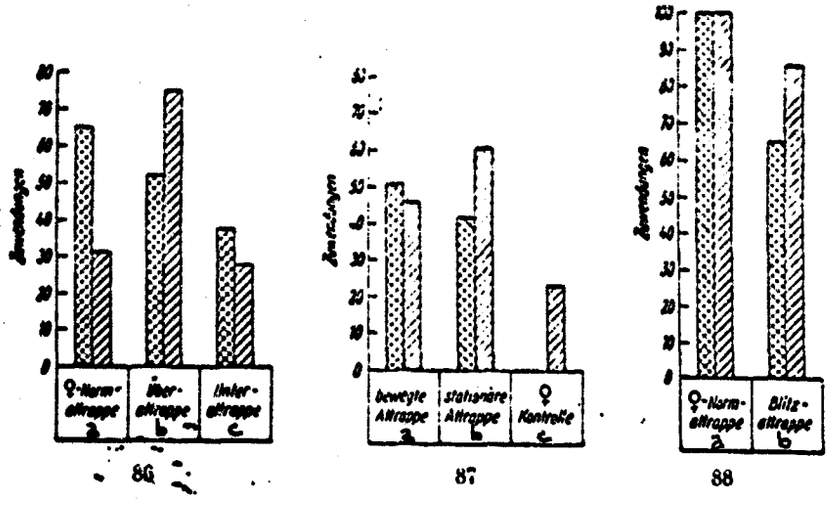
The decoys (Figure 85) were about the same amount brighter or darker than the female light for the two species. Measurement of the relatively slight intensity of these little glowing surfaces with instruments was not possible, but only a subjective comparison. The decoys were lighted with normal light (that is in the following experiments the light of a flashlight bulb with all wave-lengths of visible light).

Lampyris males prefer the intensity of the natural fe- brighter and less bright decoys. They often ran in a straight line toward the brighter decoys up to a certain distance from them, only to turn aside then or turn around, as rarely happens otherwise in their approaches, or after a normal approach they become inactive before the brighter decoy for several minutes, with retracted head and bowed prothorax; this is the same as the reaction to too strong light (cf. Chapter D I, 2a).

Phausis males always definitely prefer the greater intensity.

γ) Size as the Distinguishing Feature

In this series of experiments (Figure 86) I used oversized, normal, and undersized decoys (the normal decoy having the surface dimensions and arrangement of the luminous organs of an average-sized female). For both species the surfaces of the oversized decoys are about four times as large as the normal decoys, and the undersized decoy in the case of Lampyris is reduced by 1/3, for Phausis by 1/2. The Phausis undersized decoy also has only two pairs of points of light (as is not infrequent in nature) instead of the three of the normal decoy. — Lighting with normal light.



86 87 88

Figure 86. Light decoys: distinguishing feature size. Notation as in Figure 82. L: n = 22, N = 155; P: n = 30, N = 134. a) normal decoys, b) oversized decoys, c) undersized decoys.

Figure 87. Light decoys: distinguishing feature movement. Notation as in Figure 82. L: n = 13, N = 93; P: n = 30, N = 131. a) moving decoy, b) stationary decoy, c) female control.

Figure 88. Light decoys: distinguishing feature duration of light (constant vs. intermittent light). Notation as in Figure 82. L: n = 22, N = 164; P: n = 30, N = 185. a) female norm decoy, b) flashing decoy.

In the case of Lampyris the normal decoys get the maximum number of approaches, in the case of Phausis the oversized ones. The varying size of the luminous organs of Lampyris females due to the considerable differences in body size (less in Phausis) has no advantages in the extreme cases, which lie within the range of the light decoys used here, but not too great disadvantages, either.

d) Movement as the Characteristic Feature

The point of departure for the comparison of moving and stationary decoys (Figure 87) was the observation that unmated Lampyris females (but not Phausis females) toward the end of their lifetimes make beckoning motions with the abdomen, which bears the luminous organs. With the moving decoy pendulum motions of about 5 mm/sec were produced, approximately corresponding to those of the female, although the latter are not strictly rhythmical.

The "old" beckoning Lampyris female should actually have somewhat greater success in attracting males than the "young" non-beckoning one. Control experiments with Phausis, on the other hand, show a decrease in approaches in the case of moving light decoys. If the decoy was moved about 10 cm/sec, the number of approaches for those decoys went down very sharply with both species, an observation that I followed for about an hour but did not evaluate statistically. -- Lighting with normal light.

) Duration of Light as the Characteristic Feature (Comparison of Constant Light and Rhythmically Flashing Light)

The effect of rhythmical shining (= flashing, similar to that of species of Luciola and the American species) was to be investigated. Along with the continuously glowing normal decoy a female decoy was offered that glowed for 1/2 second per second (Figure 88). Lighting with optimal light (hereafter always yellow light for Lampyris, blue light for Phausis). -- If with the same length of flash the frequency was reduced to one flash every two seconds, the males usually interrupted their course toward the decoys with the interruption of the light.

The lower rate of approaches of both species to the flashing decoy may be attributable to the lack of the constantly effective stimulus or to the incapacity to orient themselves to the temporarily "attractionless" decoy, as has been observed with the flashing American species (Mast [82]).

ʒ) Pattern (Arrangement and Shape of the Decoys) as the Characteristic Feature

1. Regrouping and modification of the luminous fields of the female luminous organs (Figures 89a-b), lighting with optimal light. -- These important series of experiments were carried out in order to determine to what extent the patterns of luminescence of the female luminous organs peculiar to the species also constitute specific stimuli for the males of a given species. This question arose from the fact that the light emitted by the females of the two species is alike, so that its pure spectrum cannot isolate the species, and from the fact that the arrangement and formation of the individual luminous fields are quite markedly different in the females of the two species.

2. Decoys with round, rectangular, and broken luminous fields of varying size (Figure 90a-c) were compared with the corresponding female-norm decoys. -- Lighting with optimal light.

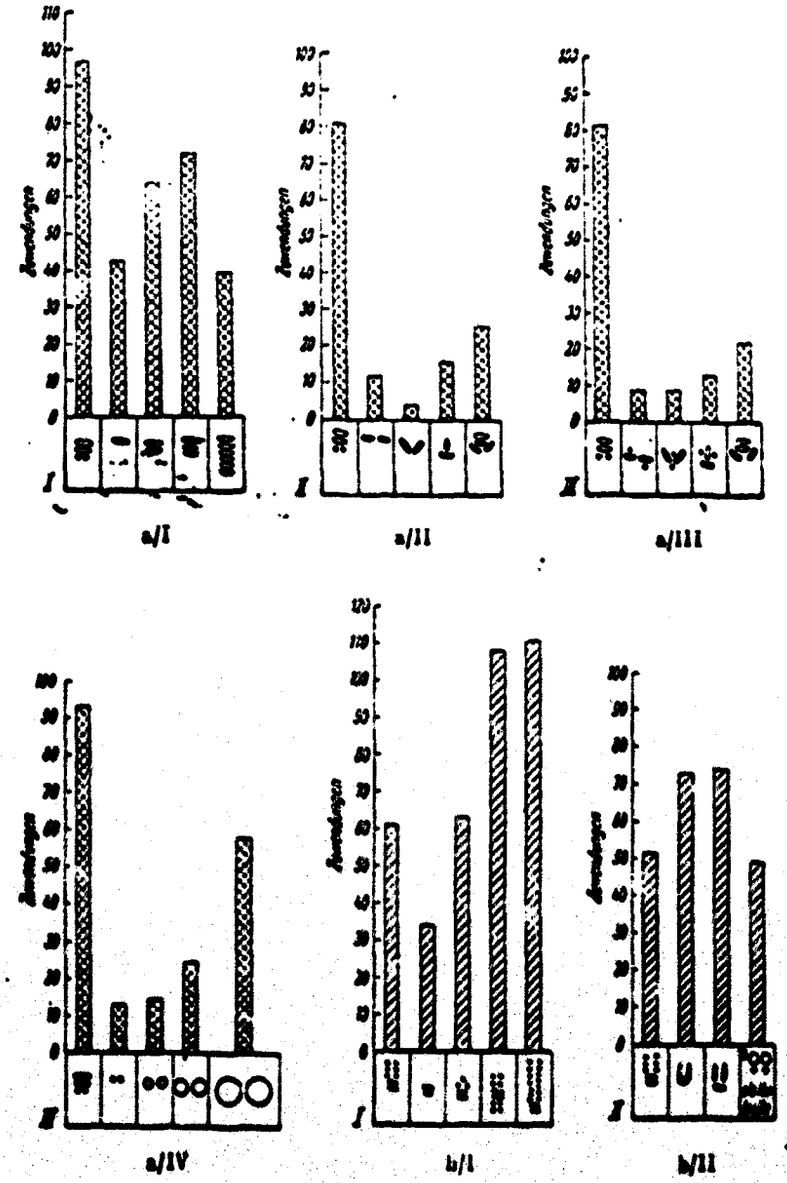


Figure 89a. Light decoys (Lasiurus): Regrouping and modification of the fields of the female luminous organs (I-IV). I: n = 33 N = 516; II: n = 12, N = 139; III: n = 10, N = 134; IV: n = 15, N = 202.

Figure 89b. Light decoys (Phausis): Regrouping and modification of the fields of the female luminous organs (I-II). I: n = 60, N = 377; II: n = 60, N = 247. Last column: two females as control.

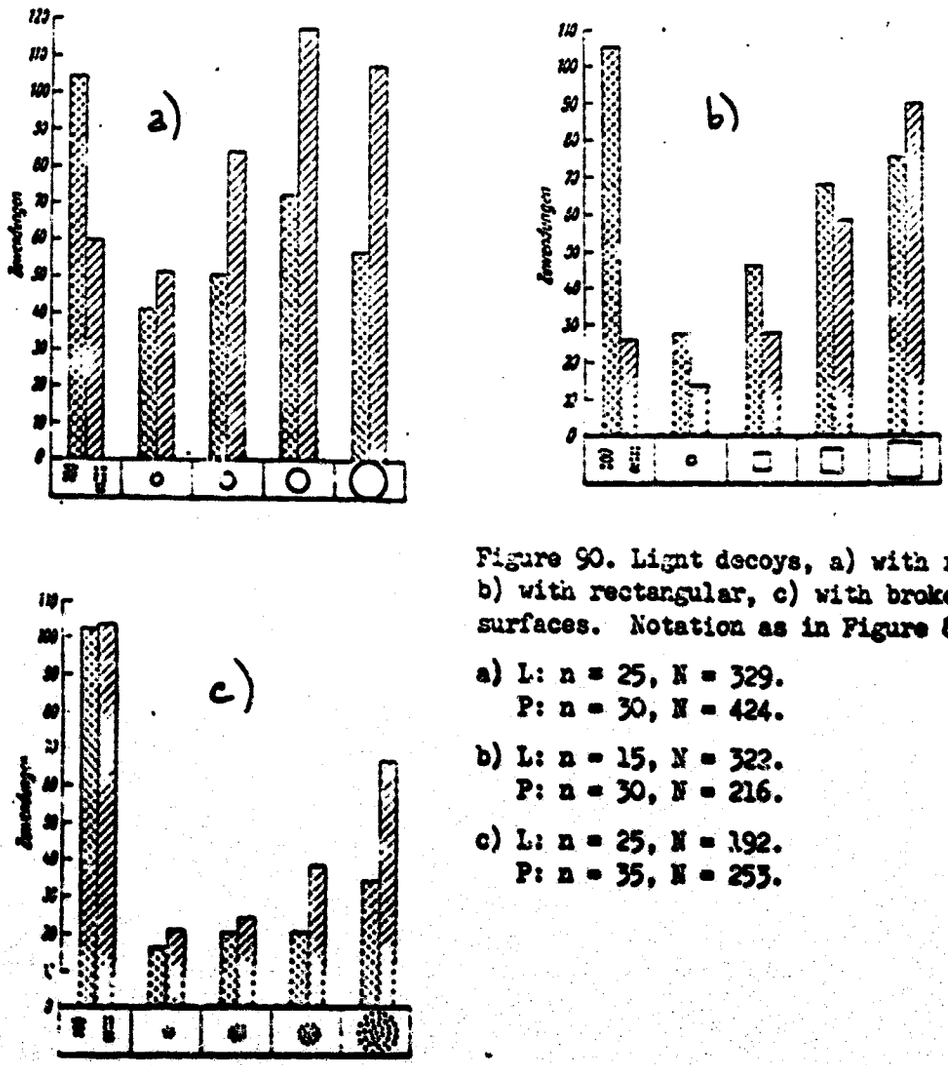


Figure 90. Light decoys, a) with round, b) with rectangular, c) with broken surfaces. Notation as in Figure 82.

a) L: n = 25, N = 329.
   P: n = 30, N = 424.

b) L: n = 15, N = 322.
   P: n = 30, N = 216.

c) L: n = 25, N = 192.
   P: n = 35, N = 253.

With Lampyris any modification or regrouping of the typical female luminous field combination causes a reduced number of approaches, especially in the more greatly modified of Figures 89a II, III, which do deviate sharply from the type of arrangement typical of the Lampyris female's luminous organ. Regroupings and simplifications of the pattern of light of the Phausis females affect their males more strongly than the normal decoy if the area is also increased; females with more larval luminous nodules may therefore be more successful.

Unbroken surface patterns of light are preferred by both species to the broken surfaces. That in the case of the Lampyris male, with its marked preference for the typical luminescent pattern of the female, the number of approaches increases with the size of the area gives grounds for conjecture that a transition to general (i.e. not absolutely sexually conditioned) positive phototaxis is taking place here, while the more intensive approaches to any large surfaces in the case of the Phausis male come nearer corresponding to our previous observations.

η) Preference Tests
(Figure 91 with Optimal Light, Figure 92a,b Normal Light)

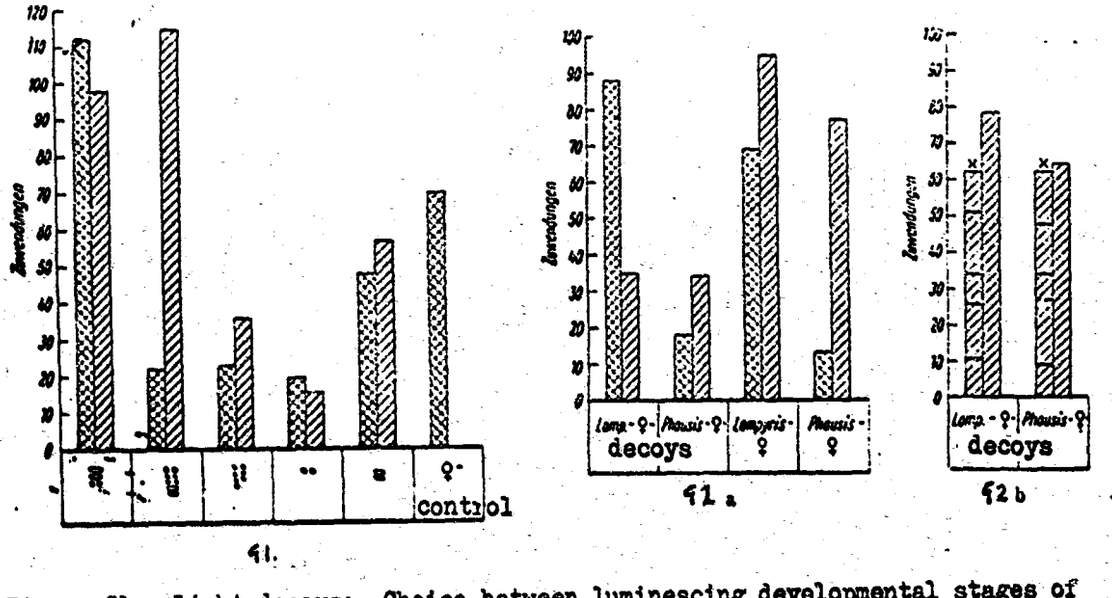


Figure 91. Light decoys: Choice between luminescing developmental stages of the two species. For identification of the luminous organs (abscissa) cf. Figure 33a-c. Notation as in Figure 82. L: n = 26, N = 295; P: n = 30, N = 322.

Figure 92a. Choice of males of the two species between female light decoys and genuine females of the two species. Notation as in Figure 82. L: n = 47, N = 188; P: n = 40, N = 241.

Figure 92b. Choice of the Phausis male between Lampyris and Phausis female decoys (n = 35, N = 124). The columns marked X are a compilation of results obtained at different times. They show that the results always remain almost in the same proportion. Such controls, though used in other cases, are not shown in the other graphs.

The figures (91, 92a-b) confirm what was suggested in 1: The Lampyris males "recognize" quite well the proper arrangement of the luminous fields of their females. They can hardly confuse the other luminescing developmental stages of the two species (for the identification of these cf. Figures 33a-e) with their females (Figure 91). The fact that Phausis male luminous-organ decoys are relatively much frequented may be explained by the fact that they resemble the luminous organs of small Lampyris females (if we disregard the little, dot-like pair of luminous organs carried over from the larval stage).

Phausis males on the other hand cannot distinguish between their own and Lampyris females; the decoy experiments confirm in this respect the observations often made in the field (see page 118). Before the glowing larval stages of the two species the number of approaches drops off; their light, coming on erratically, must rarely lead males astray in the field as well, — at any rate I never was able to observe it. The glowing Phausis males are equally rarely approached, since they fly themselves. (On this point cf. 1 c ♂).

On the light decoy experiments the following may be said in summary: The first reaction in the stimulus-reaction chain of sexual behavior, t' approach flight of the males, leads reliably to the goal, namely to the female of the same species, only in the case of the Lampyris male. Here the conditions of the female light, such as maximal luminous energy in the yellow range, intensity, size, and arrangement are optimal. Deviations from this norm yield inferior results, monochromatic yellow light when combined with the other characteristics of the norm yields above-normal ones.

Any visible light will serve to trigger the approach flight of the Phausis male (as long as it is not strong enough to bring about negative phototaxis), quite independent of the arrangement of the luminous fields. The wave-lengths strongest in the light emitted by their females have an optimal effect, although other colors of visible light precipitate the reaction quite well. Blue light, which occurs nowhere in the emission spectra of the species studied, has an above-normal effect. This explains why Phausis males cannot distinguish their own from Lampyris females. This defective performance, which is not insignificant in view of the short lifetime of the imagines, may be compensated for by overproduction of males.

2. Excitatory Effect of the Female Odor

From the above it is clear that flight toward the female odor — if it occurs at all — can only be conceded a minor

rôle, although the Lampyris females at least give off a clearly perceptible, somewhat cabbage-like odor.

The above-described attempts at copulation by the males among themselves, which at least in Lampyris are initiated without the influence of light, copulations with non-glowing females that the males encounter accidentally, and the whole foregoing chapter do not rule out any olfactory influence either in the males' approach flight or in the rest of the sexual behavior.

The following experiments were carried out with both species under as nearly natural conditions as possible, with weak, diffuse, non-disturbing light in the laboratory.

1. Freely moving, non-glowing females and females with luminous organs covered or darkened with black lac were not approached by flight (even in the field). -- But if such females were approached by the males within about 5-15 mm, sudden searching movements of the male usually brought about a contact very quickly, and this in turn led to coitus.

2. Females that had been dead for forty hours and were in fact slightly putrefied induced sexual behavior in the male, which usually ended with a normal copulation of normal duration.

3. Female parts (head, thorax, abdomen, and entrails respectively) were arranged in a circular pattern (5-7 cm in diameter) and males ready to mate set in the center of the circle. In every case the males when they came upon the female parts showed a behavior clearly deviating from the normal movement: Staying on the spot with vibrating movement of the antennae, cautious feeling over the female parts; finally the males ran alongside the parts and at fairly large abdominal parts actually unsheathed the penis -- all indications that a female odor is quite well perceived and has a sexually exciting effect. Still more definite was the sudden change in behavior when males running free and in straight line outside the radius of the odor suddenly encountered it. -- The males showed similar reactions to fresh-laid eggs.

4. The following series of experiments, carried out only with Lampyris, will be discussed in part in the next chapter. I attempted to study the selective effect of the female odor of particular regions of the body and at the same time the sexual effect of particular bodily shapes of the female by the use of mutilated females.

a) Isolated female head + prothorax: attention for minutes, with lively feeling and rapid movements as at the beginning of copulation; the penis is not protruded.

b) Isolated mesothorax and metathorax: as in a), but less long and intensive.

c) Isolated abdomen: rapid and correct orientation, complete normal copulation as with the normal female (duration 9-17 minutes) (Figure 93).

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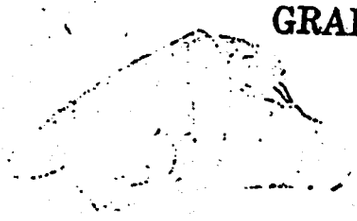

Figure 93. Copulation with isolated female abdomen (Lampyris).

d) A female without the last three abdominal segments: as in c), but with shorter duration. The penis is introduced into the open end of the abdomen and withdrawn several times in rapid succession; the female is then soon abandoned.

d) The fore end of the female (= head + thorax and legs) was replaced with the rear end (= last three abdominal segments): result as in c). -- The description of the results of this series refers to Lampyris.

Phausis males ready to copulate react to fragments of their females much more powerfully and intensively; even female entrails bring about protrusion of the penis. In spite of the fact that in all the above individual experiments the normal copulation behavior of the male was induced, however, copulation was achieved less frequently than with Lampyris.

The female odor is thus not a remote stimulus for the approach flight of the male, but doubtless contributes greatly to intensifying the sexual reaction to the female. In particular it apparently makes possible orientation to the female, although we cannot say what bodily parts of the female serve this purpose (cf. the next chapter). The external female sexual parts, which the long-waiting female protrudes (see page 95) cannot be considered responsible for it, for even without them the normal sexual behavior leads to "copulation" (cf. 4d).

3. Excitatory Effect of the Female Bodily Form

After the results of the preceding chapter the question arises whether the mere form of the female plays a definite rôle in the sexual behavior. In that line the following results were obtained:

1. Females fixed in alcohol for a year were offered after repeated washing in sterile distilled water to males ready for copulation. These lifelike form "decoys" induced no approaches or other reactions.

2. These decoys were smeared with material from mashed females. They then had the same effect as the "odor rings" (see preceding chapter), and in addition were occasionally mounted with protruded penis.

3. Plasticine imitations of the female shape had no effect on the males.

4. Plasticine imitations that were smeared with material from mashed females or the end of which was dipped into a severed, mashed abdomen of a freshly killed female had the effect described in 2.

5. Combinations of plasticine fore end with female rear end and plasticine rear end with female fore end had the effect described in 2 or as in 4c (preceding chapter).

6. Females were surrounded with cylindrical plasticine shells so that only the fore end and the rear end (= the last two abdominal segments) remained free. No matter from what side the male approached this "semidecoy," orientation to the female and copulation ran normally in every respect, although the male as he moved backward to hunt for the female copulative opening completely lost feeler and tarsi contact with the big female (Figure 94).

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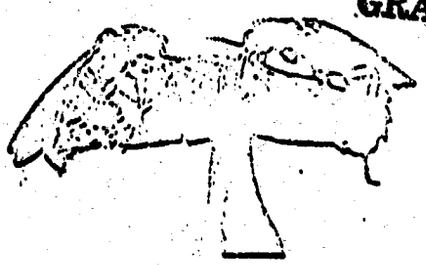

Figure 94. Copulation (and attempt at orientation) with a female surrounded with a cylindrical plasticine shell (Lampyris males and females).

According to these findings the shape of the female body appears to be largely secondary for the sexual behavior. It may also be stated on the basis of these experiments and various ones described in the previous chapter that it plays no part in the orientation either.

4. Combination of Light and Form Decoys

An attempt was made to clarify the question whether

the female bodily form in connection with a light decoy has an excitatory effect. The female form in question was about 5 mm away from the light decoy. The following experiments were carried out with both species.

1. Female light decoy + non-glowing living female: The light decoy was approached first; only through chance contact with the female did a copulation come about.

2. Female light decoy + dead female: result as in 1.

3. Female light decoy + female preserved for a year in alcohol and washed for days: approaches only to the light decoy.

4. Female light decoy + plasticine imitation of the female: result as in 3.

5. For Phausis males a glowing Lampyris female decoy was combined with a non-glowing Phausis female. Result as in 1.; the Lampyris female light decoy was approached first. When the female was accidentally found, attempt at copulation. If the female ran away, the male left her and went back to the Lampyris female light decoy. Return to the light decoy when the female of the male's own species ran away was also occasionally observed in experiment no. 1.

6. The combination of Phausis female light decoy and non-glowing Lampyris female had no success with Lampyris males.

5. Excitatory Effect of Movement Stimuli During Approach and Copulation

As described in Chapter D I 1, the female hardly makes specific excitatory movements in the course of copulation attempts and during copulation. Since copulation with dead females is possible, it appears that no essential mechanical movement stimuli come from the females. Some stimulus is necessary, however, that induces the female to give up the typical glowing posture and assume the normal walking posture without which copulation is impossible. This change comes with tactile stimuli at any point when a male approaches the female. — The mechanical stimulus of the searching movements of the penis induces the female to raise the tip of the abdomen, and this facilitates copulation; in the case of dead females the copulation attempt takes longer. In addition the vibratory motions of the male's antennae, which are directed predominantly toward the fore end, especially the head, appear to induce the female to stay on the spot. This may be observed e.g. when a male is brought to a running female during the active period. Experimentally, too, the locomotion of a female may be stopped by touching the fore end lightly but with high frequency with a soft brush. In attempted copulation of Phau-

sis males with Lampyris females the female takes to flight, evidently because the smaller Phausis males cannot provide this stimulus. All the above tactile stimuli can be experimentally provided successfully with females willing to mate.

Along with light and olfactory stimuli these movement stimuli appear to be not entirely without significance. In any case the movement-stimuli reaction chain between male and female accelerates the undisturbed course of the sexual relations (compared with copulations with dead females).

Annex: Attempts at a "Male Pattern"

The relatively great passivity of the females in the choice of partners does not in itself mean that there is no "male pattern" for the females. The Phausis males, equipped with splendid luminous organs, come in for special consideration in this respect, especially as it is precisely their females that possess in the prothorax, which covers the eyes, two large transparent (completely pigment-free) windows, such as are otherwise known only in the males of the two species, but not in Lampyris females. On this point I did the following experiments:

1. In both species: If CO_2 narcotized or freshly killed males are presented to females ready to mate (in the glowing posture), nothing at all shows up in the behavior of the females that would justify inferences as to a sexual "affect."

2. In Phausis: a) Glowing Phausis males immediately before the eyes of females ready to mate (i.e. exhibiting complete sexual appetency behavior).

b) Non-glowing males in the immediate vicinity of females ready to mate, but not touching them.

c) Material from mashed males in immediate vicinity of females ready to mate, but not touching them.

d) Male light decoys (which see) in varying intensity before the eyes of females ready to mate: With too strong intensity of the decoy light the females give up the glowing posture, and when subjected for long to the effect of the light they seek out hiding places (cf. phototaxis, Chapter D I 2).

All these attempts to find out something about the effect and significance of the Phausis male light were completely without results; neither an optical nor an olfactory effect on their females could be demonstrated.

On the analysis of the "female pattern" the following

may be said by way of summary:

The sexual appetency behavior of the two species agrees in the main. Any effect that isolates the species and reduces errors in the choice of partners must therefore be looked for primarily in the grouping and choice, typical of the species, of definite key stimuli (the inherited excitative mechanism) and in morphological and physiological differentiations.

1. The inherited excitative mechanism for the approach flight is simply the light emitted by the female, which for for Lampyris males must not only have a definite quality, but also be radiated out in a specific surface arrangement. Phausis males react to very unspecific light and consequently confuse their females with those of Lampyris. Certain light decoys operate as supernormal stimuli. Odoriferous substances of the females play no part as remote stimuli for the approach flight.

2. The inherited excitative mechanism for orientation to the female, for protruding the penis, and for the actual copulation appears to be based on restricted components of an olfactory and tactile nature for both species. The olfactory component is superior to the tactile. Since decoy experiments with natural odoriferous substances are difficult to carry out, I can make no detailed statements as to the specific inherited excitative mechanisms. It is not possible to localize specific stimulative odoriferous substances in definite bodily regions of the female, but odoriferous substances are nevertheless certainly important stimuli at close range. -- The overall form or the form of specific parts of the female body are not to be credited with any stimulative effect when isolated from other components.

3. A specific "male pattern" appears to be lacking in the females of both species.

III. Discussion

The rhythm of activity and luminescence of the imagines serves exclusively the purposes of reproduction and is part of the sexual appetency behavior, for outside the active-luminescent phase the males do not react to light decoys of otherwise above-normal effect (not even when -- in order to exclude any fatigue of the corresponding reaction-specific energy -- males are used that have not before copulated or been used for decoy experiments). Gradual ineffectiveness of key sexual stimuli, presented naturally or artificially, after a certain period of good effectiveness coincides with the end of the active phase. Since the studies of the normal diurnal rhythm of activity and luminescence of the imagines were carried out without any in-

fluence of key sexual stimuli (cf. Chapter D I 1a), in the ineffectiveness of the inherited excitative mechanisms for the search for the glowing female or the luminous decoy we are not concerned with exhaustion of reaction-specific energy, but with the end of the phase of activity and luminescence, conditioned by inherent factors. While the approach flight of the males, which can be often repeated, thus appears to consume little reaction-specific energy, on the other hand the final act, copulation, can less often be repeatedly induced.

One might at first be inclined to interpret the attraction of the males by the female light by saying that the positive phototaxis observable in many nocturnal insects is utilized here in the sexual appetency behavior. The change from positive to negative phototaxis at "purposelessly" high luminous intensities regardless of color might be regarded as evidence in favor of this interpretation. This and the physical similarity of the emission light of the females of both species (and all developmental stages) makes further stimulus screening mechanisms necessary. My decoy experiments with both species showed that only a few characteristic key stimuli have an effect on the corresponding inherited excitative mechanisms. The central nervous "screen" between light-sensitive organ and motor center is finer and better differentiated in Lampyris males than in Phausis males, so that the latter on their approach flights often confuse their females with those of Lampyris; it might also be said that the "Lampyris female pattern" is also contained in the stimulus screenings of the Phausis male. The sharpness characteristic of the lock and key system for Phausis thus appears to be much attenuated, and this may be "compensated for" by the overproduction of males of this species and by the morphologically conditioned impossibility of copulation with Lampyris females (cf. Chapter E II 3).

Phausis seems less highly specialized than Lampyris in various respects (ethologically and morphologically: Phausis females e.g. with prominent rudimentary wings, which bring them closer to the normal beetle type; pigmentless prothorax windows, such as belong to the males of both species), and probably is closer to the original type of lampyridae (with sexes showing no great sexual dimorphism).

From this phylogenetic standpoint the imaginal luminous organ of the Phausis males, which has become sexually functionless, appears understandable, for, as is well known, the other lampyridae, which are not sexually dimorphous or not so much so, still have imaginal luminous organs in both sexes. Buck [23], to be sure, considers that it is they, which find each

other by means of a mutual flashing signal duet (see below), that are to be regarded as derived forms in comparison to the lampyridae with continuous or intermittent luminescence.

The sexual behavior of the few lampyridae thus far accurately observed (chiefly American species) is different from that of our native species. They all seem to belong to the same light-emission type, namely the flashing type (see page 87). Buck [19-21], Hess [58], Mast [82], and McDermott [83-88] agree in reporting that the females respond exclusively to spontaneous flashes of the males or (not in all cases) to artificially (with pocket flashlights, matches, and the like -- Buck, Mast, McDermott) imitated flashes with flashes of their own. The males then orient themselves immediately toward the flashing females (and according to Mast not to artificial light) if the answering flash of the female follows the male flash at the interval of time characteristic for the species. Through repeated signaling and continued orientation of the males the meeting and copulation finally come about. The females (according to Mast) constantly turn the abdomen, equipped with the luminous organs, in the direction of the flashing males. These lampyridae never respond to continuous light (of artificial sources of light) (Mast, McDermott). The southern European Luciola species (Emery [37, 38] and my own observations, unpublished) belong to the same flashing type.

The sexual appetency behavior of these flashing and our slowly intermittent glowing types (in Buck's sense) is thus basically different: In the former the males spontaneously flash in a definite rhythm and their otherwise non-glowing females answer by flashes. In our species the females glow without the influence of the males throughout the activity cycle continuously and in a typical motionless glowing posture. The optical situation that induces the final act, copulation, is thus also different: For the flashing species the time relationship between male and female flash and the duration and nature of the flashes is typical (Figure 95). Since in our species neither the males nor their light (if it occurs visibly at all) affects the females and the female light of the two species is not different, the system of stimuli must look different. While both sexes of the flashing species are extraordinarily active, in our species the females have a largely passive behavior.

This difference in the sexual behavior of the two groups has not been considered previously. Instead the observations of American lampyridae have simply been transferred in an inadmissible way to all lampyridae. But the almost exclusively descriptive observations of the sexual behavior of flashing

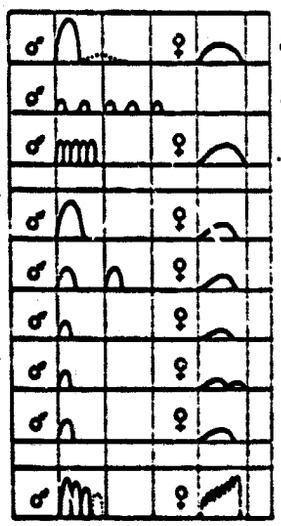

Fig. 95. Chart showing relativ intensities and durations of flashes of American Lampyridae (1 cm vertically equals approximately 0,02 candle power; 1 cm horizontally equals approximately one second in length of curves; space between curves representing flashes of male and female of some species, is arbitrary.

(After McDermott [87], Figure 6, page 58.)

lampyridae (with the exception of Photinus pyralis, which Buck [21] studied more accurately experimentally) will only have the value of preliminary studies until they are followed up by more exhaustive experimental analyses. Such analyses seem all the more to be desired in view of the fact that often several species inhabit common biotopes and that — as shown by Figure 95 and Table 16 — many species do not differ essentially in rhythm of flashing, in duration of flashes, or in the spectral range of the light emitted. Besides mechanisms to isolate the species we should expect to find in the flashing species a "female pattern" and a "male pattern," since for both sexes an active reaction to light is prerequisite to their meeting. We are still far from a precise knowledge of the specific inherited excitative mechanisms of the various emission types of lampyridae.

B. Supplementary Observations

I. On Larvae

1. Akinesis

The larvae of both species fall into akinesis upon mechanical stimulation, especially of the cephalothoracic region (touch, agitation, etc.). — In Phausis after mild stimuli the bodily posture remains unchanged, but after ruder stimuli the insect curls its body more or less semicircularly, draws in the extremities, and falls on its side or back. On its back or side the larva always falls into akinesis in the posture described. Motionlessness and inhibition of correction of the posture may last for hours. (Very inconvenient in experiments!) — In Lampyris akinesis is not so pronounced. In contrast to Phausis it almost always assumes a side or back position and is bent in a semicircle. The duration is restricted to seconds or at most to a few minutes. Grasping reflex and righting reaction are absent in both species.

With repeated stimulation the state of akinesis becomes

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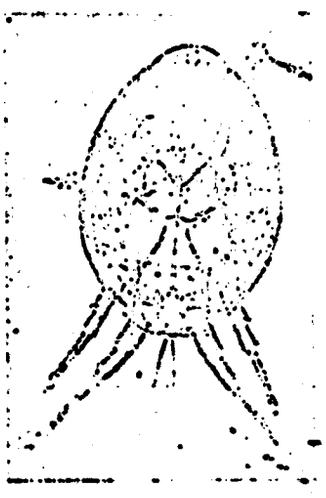

Fig. 96. Unidentified ectoparasitic mite, a parasite in my larva-growing experiments.

shorter and shorter; the reaction tires. Mechanical, chemical, and thermal stimuli at an intensity exceeding a certain threshold may reduce the duration of akinesis or eliminate it entirely. Strong mechanical and thermal stimuli applied to the tarsi and the abdomen and to the meso-thoracic sternite have an especially antagonistic effect.

In the imagines there is no akinesis.

2. Enemies

The chief parasites in my growing experiments (for Phausis and Lampyris) were mites [see Note] (Figure 96). Sometimes up to 80% of the fireflies were infested, the rest being for the most part freshly molted or freshly captured outdoors. The larvae were often infested with enormous numbers, especially at the soft neck part, the mouth parts, and the feelers; other, less preferred places were the legs, the anal region, and the intersegmental membranes. The mites sucked mostly at the soft integumental parts (such as intersegmental membranes, hair follicles and the like). Heavily infested larvae died after a short time. -- In the growing vessels the still unattached mites were usually to be found on elevated places with the first pair of legs extended upward and groping. Presumably the mites first attached themselves to the feelers and legs of the beetle larvae, to look for secure places on the host's body later (neck fold, joints, and intersegmental membranes). The mites possess a suction-cup-like process at the posterior end. I attempted to combat this plague mainly by keeping the growing vessels clean and occasionally sterilizing them, and by isolating the larvae just molted and still uninfested. Removing the tiny mites (160 µ in length) from the larvae was time-consuming and taxing; it could be done only under 50 to 80-fold magnification, and of course only on narcotized larvae.

[Note] The mites have not yet been identified.

More rarely the larvae of both species were afflicted with nematodes [see Note], which lived parasitically in the head and neck of the larvae and caused parasytic symptoms first of the infested parts of the body and then of the whole insect, resulting in death.

[Note] The worms were sent in for identification and unfortunately lost.

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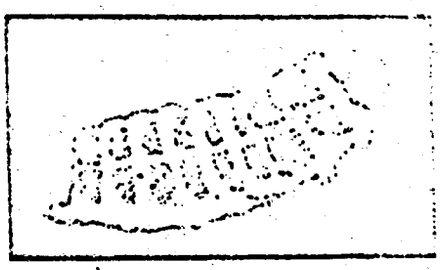

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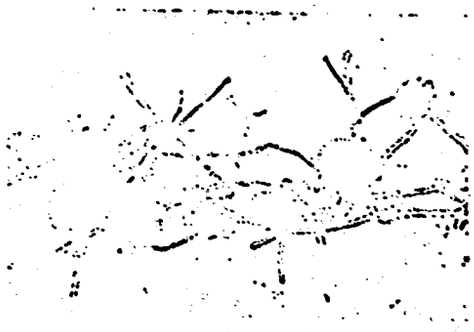

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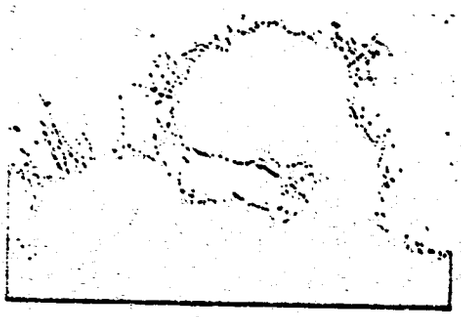


c

Figure 97. Damage to Lampyris larvae by endoparasitic fungus (Beauveria bassiana Bals., Vuill.).

Figure 97a. One day after the death of the larva the fungus mycelium, previously not visible externally, has grown through the softer parts of the larva's body.

Figure 97b. Sporophores of the fungus outside the body of the larva.

Figure 97c. Balls of fat of the larva's body, grown through with a fine, dense mycelium at the time of the larva's death.

Especially in the fall and winter fungi (Beauveria bassiana (Bals.) Vuill. [see Note]) were a devastating plague in Lampyris larvae with fatal effects. The first symptoms of attack could not be detected until after death, when on the same day that death occurred a soft fungus mycelium grew out of the mouth opening or between the mouth parts and at the anal region. In this stage the body of the insect is noticeably hard and stiff. After one day (Figure 97a) the mycelium has grown through all intersegmental membranes and overgrown the whole body; this process is accompanied by guttation, which disappears during the subsequent sporophore formation (Figure 97b). At about 17° C this sets in after 5 to 7 days and manifests itself macroscopically in a yellowish tint. -- Afflicted larvae in a living condition cannot be detected even 2-3 days before the first visible signs of fungus growth, since they show no deviation from normal behavior. Insects dissected immediately after death show that the viscera, fat bodies, etc. are completely grown through by a finer mycelium than the externally visible one and form a matted, compact, but at the

same time brittle mass, the external organ complexes still being quite recognizable (Figure 97c). I found none of these larvae afflicted with parasites in the natural habitat.

[Note] I am indebted to the Federal Biological Establishment for Agriculture and Forestry (Institute for Biological Pest Control), Darmstadt, Kranichsteinerstrasse 61, for identification of the fungus.

In the literature there are extremely varied interpretations of the luminescent function of the larvae with regard to its biological significance. Many authors come out in favor of a protective function, others against it. In its favor it has been pointed out that the females, which need protection most, glow most strongly (Dieckhoff [34]), that predators would not like to snap at "sparks of fire" (Haupt [57]), that the free-flying species luminesce intermittently, and only the wingless ones, which live mostly hidden in foliage and the like, luminesce continuously and permanently (Olivier [96]). On the other hand Knauer [68] and Vogel [131] reject the repulsing function of the light, saying that frogs, toads, spiders, and bats are not frightened away by it. -- I could find no reports of experiments on this question, and since I needed my insects for other purposes until the completion of this article, I could not carry out any experiments, either. Studies with glowing larvae are also very difficult, since they normally glow very capriciously (except during the rest periods before molting, which see); pupae would be better suited to this purpose. -- I think the luminescence could have a protective function only in Phausis larvae, and not in Lamprohiza larvae, since they let their light go out pretty quickly in response to mechanical stimuli. In any case they should be well protected by akinesis, by protective coloration, and by their hidden way of life.

3. Extirpation of the Luminous Organs; the Symbiosis Problem

Statements in favor of a symbiosis with luminous bacteria in lampyridae (cf. also pages 36 ff.) have been made by Kuhnt [70], Piérantoni,* and Zirpolo;* this is opposed by Czepa [32], Harvey [52,53,55], Hasama,* Meissner [90,92], Verhoeff [126], Vogel [130], and Weitlaner [137], while Buchner awaits further studies and appraises the problem cautiously [15-18]. The opponents base their position either on unsuccessful attempts to grow luminous bacteria or on indirect physiological experiments which rule out any luminescence symbiosis.

*Cited according to Harvey [55].

Harvey [52] extirpated the luminous organs of firefly larvae, and raised three of these to imagines. These imagines

were all equipped with normal imaginal luminous organs. From this experiment Harvey concluded that luminescence is a fundamental characteristic of the photogenic cells, which is founded on the chemical production of luminous material, since the imaginal organ is newly formed. In case of symbiosis, after removal of the larval luminous organ no luminescence would be expected in the adult insect, since no other region of the larva glowed, — unless we assumed a non-luminescent stage in the life cycle of the bacteria.

I repeated the experiments with larger numbers of female Lampyris larvae (30 individuals). The larvae were operated on on one side and on both sides. During the experimental period four larvae underwent the molting into the imago. In checks made both subjective-optically and photokymographically no luminescence could be discerned in larvae operated on on both sides, but in those operated on on one side luminescence of the intact luminous organ was observed.

The larval organs were not regenerated after several moltings (up to four). In all the larvae the normal imaginal luminous plates developed during the pupal stage (as was afterwards proved histologically), and they glowed. The larval luminous organ of the specimens extirpated on one side of course were retained in the adult insect.

Harvey's findings, which were somewhat unsure because of the small number of subjects, are thus confirmed for Lampyris by my experiments. On the basis of these experiments and the physiological experiments concerning the luminescence of the lampyridae, especially those of McElroy and Strehler (both cited according to Harvey [55]), I do not consider the luminescence of the lampyridae symbiontic, either.

4. Peculiarities of Locomotion

Because of the fact that the relatively small, weak legs have to move an abdomen that in the case of Lampyris is especially long, there are among the larvae peculiar modes of locomotion, which appear also to be quite useful in the pursuit of snails. The well developed pygopodium is used by Lampyris larvae not only as a cleaning organ, but also in almost all cases for measuring-worm-like locomotion; in the differently built Phausis this is less the case. With the pygopodium the larvae can creep backwards quite agilely. — The strong bristles on both sides of the rear corners of the second to eighth abdominal sternites are considerably prolonged in the anal direction (especially the last three pairs) and arranged obliquely toward the rear. During the looper-like movements they can assist the pygopodium as organs of locomotion. (On

the function of the bristles cf. also page 41).

5. Repair, Regeneration, Viability

If it is difficult to raise larvae, that is not due to any lack of hardiness, or viability, for their viability is astonishing. Decapitated Lampyris larvae run around for more than two months (at about 18° C) with such normally coordinated walking, looping, and retrograde movements that they are indistinguishable from uninjured larvae. They perform normal righting movements, but do not fall into akinesis. Decapitated Lampyris larvae without intestinal tract behave in the same way, but not for so long a time. This astonishing behavior is to be explained chiefly by the fact that for lack of space the cerebral ganglia are located in the prothorax and so are not removed by decapitation.

They stand severe wounds, bruises, amputations of bodily appendages, operations on the inside of the body with great loss of blood so well that after a few hours they can again attack snails. Wounds heal very quickly. Extirpations are apparently not made good in the course of moltings.

6. Perception of Drafts, Thigmotaxis

The larvae react very sensitively to the slightest currents of air (especially Phausis). They immediately become motionless and cling fast to their support with feet and pygopodium.

To air currents, very slight concussions, and tactile stimuli just too slight to bring on akinesis the larvae react with negative thigmotaxis and recede from the stimulus with suitable mody movements. Larvae meeting or otherwise touching each other show no such reactions.

During their daily inactive period the larvae show a strong positive thigmotaxis. In the absence of obstacles the larvae press against their support; they also like to force themselves into corners of the vessels they are kept in (cf. the paths shown in Figures 20a,b) and into all sorts of openings (even at night or when the opening is formed by translucent material; negative phototaxis is thus ruled out in these cases). This positive thigmotaxis often hampered the carrying out of experiments. In the larvae living at liberty it is no doubt connected with the sensitivity to external stimuli of all kinds, for by positive thigmotaxis the animal is protected in its preferred habitat against drying out, angainst light, and other influences.

7. Righting Movements

If larvae under normal conditions (in climbing, in the capture of prey, etc.) get into a prostrate position on a flat, rough surface (e.g. filter paper), they try in two ways to re-establish contact with the tarsi: a) Head and body are maximally extended, the legs make groping movements, and fore and rear portions of the body are raised from the supporting surface and twisted around their longitudinal axis to the supporting surface. This turning movement only occasionally succeeds; in that case the animal then falls into the normal position and immediately holds fast. This sort of twisting often continues for several minutes.

b) If after long attempts a) does not lead to turning over, with lightning speed posture a) is changed to posture b): The fore end and the abdomen press against the supporting surface with a slight elevation of the central portion of the body, and the larva flips over sideways and gets into its normal position by using the pygopodium and tarsi. This reaction usually leads to the desired result within a second.

It is remarkable that a) is always executed first, for this reaction under normal conditions usually leads to the legs or the pygopodium again finding contact. -- That the efforts to turn depend on a contact of the tarsi and pygopodium with the support is apparent when tarsi and pygopodium accidentally touch each other during the semicircular curling of fore end and abdomen and hold fast to each other for a while. The larvae often remain in this posture, so that further turning movements are ruled out.

II. On Imagines

1. The Question of Nourishment

According to Czepa [32] and Weitlaner [138] the imagines eat humus, the Lampyris females also eating green plants; according to Maille [78] they are herbivorous, according to Reoluz [110] both herbivorous and carnivorous (snails); Acloque [1] and Newport [95] report the taking of nourishment only in the case of females (Newport without mention of the type of food, Acloque mentioning snails); Höllrigl [62] was never able to observe taking of nourishment by Phausis imagines. -- According to my observations the imagines of both species take water.

The following observations and considerations tell against the taking of nourishment by the imagines of the two species:

1. The reduced mouth parts: in Phausis while the development typical for the larvae is retained, mandibular

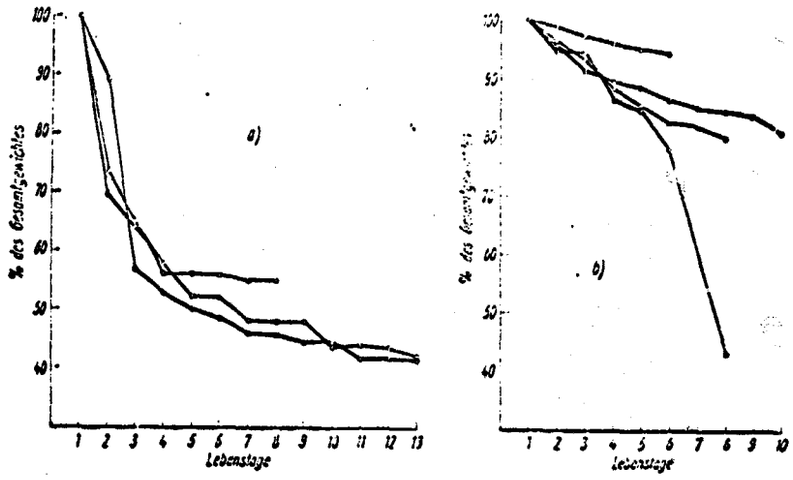


Figure 98. Decrease in weight in the course of the lifetime of the imagines (Lampyris): a) in males until their death, b) in females until the beginning of egg-laying. Vertical scale: % of total weight. Further explanations in the text. Horizontal scale: days of the [imaginal] lifetime.

canals, etc. are lacking; in Lampyris they are reduced to tiny rudiments.

2. The activity cycle: The imagines are completely inactive in the daytime, and at night they show only sexual appetency behavior (cf. Chapter D I 1).

3. The empty intestine (even in freshly captured specimens): The intestinal tract seems reduced as compared to that of the larvae, but otherwise still fully developed.

4. The fact that the fat bodies are used up by the end of the lifetime.

5. The fact that specimens kept from the pupal state until death between filter paper without nourishment of any kind lived just as long as imagines kept in growing vessels arranged as true to nature as possible with abundant provision of snails. (Imagines show no reactions of any kind to snails!)

6. The weight of the living insect declines progressively down to a certain percentage (Figure 98a,b), after which "natural" death occurs. This death could of course be interpreted as "death from starvation." The experiments whose results are shown in these figures were carried out in a largely natural habitat at 100% relative humidity and 21° C. It is to be noted that no open water was available to them, as they take water greedily (10-20% of their body weight).

The fact that the curves for the males fall off rapidly at first is to be attributed to their incomparably greater activity. Curve I of Figure 98b represents the decline in weight of a female that laid all her eggs (unfertilized) between the sixth and seventh day and died on the eighth day of her life. This curve shows that the net weight of the females (without the egg ballast) also declines 50% by the time of death. The other curves of Figure 98b were broken off at the beginning of egg-laying.

2. Enemies; Phoresy

The females, many of which I was able to observe in the field from the first day of their appearance until the natural end of their lives, appear to have few or no enemies. I offered glowing females to toads, which ate them. -- The males on the other hand are found by the dozens in spiderwebs, where they are sucked dry by spiders. I offered non-glowing imagines of both sexes to a bat (Selysius bechsteini) that had been without food (at 21° C) for several days. Only during a meal of meal worms did it happen that the bat started to eat a firefly or actually bit into one, but then flung the bite away. When not given meal worms with them, the bat did not react at all to the fireflies offered. Perhaps their unpleasant smell has a repellant effect.

I observed phoresy on a copulating Lampyris pair that were covered thickly all over their bodies with uropodidae.

3. Morphological Comparison of the Penes and Laying Apparatus in Lampyris and Phausis

Verhoeff [125] describes only the abdomina of Phausis males and Lampyris females, so that comparison of the two species and the two sexes was not possible. The necessity of such a comparison presented itself to me through the fact that Phausis males not only flew up to Lampyris females, but also attempted to copulate with them. Would such a copulation be possible in theory? Figures 99 and 100 represent the morphological relationships of the penis and the laying apparatus in the two species. The penis and the female genital opening are essentially simpler in form in Phausis than in Lampyris. The lack of the grasping apparatus peculiar to the species may make fixation in the female genital opening of Lampyris impossible for the Phausis male. The dorsal process of the ninth segment of the Lampyris female also seems to be a hindrance to copulation, for in the attempt at copulation the Phausis penis during the hunting movements does not penetrate into the genital opening of the Lampyris female at all.

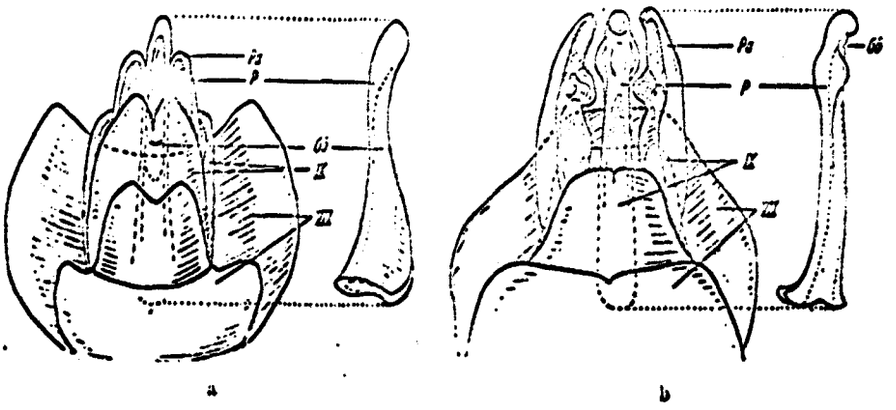
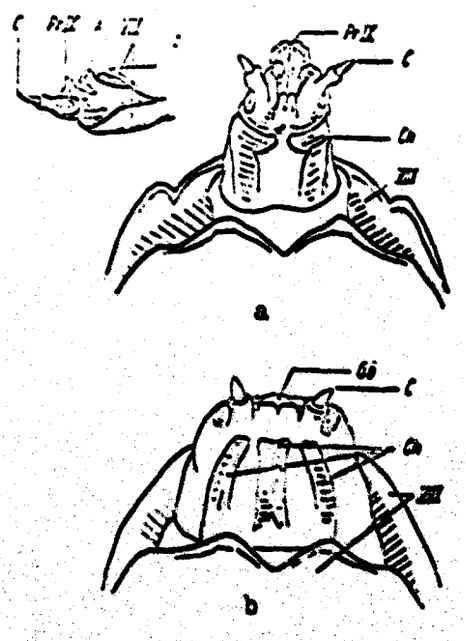


Figure 99. Male sexual appendages of Lampyris (a) and Phausis (b). (Hair omitted.)

Figure 100 (right). Female sexual appendages of Lampyris (a) and Phausis (b). (Hair omitted).



Legend for both figures:
A anus
C cercus
Ch chitinous plates
GÖ genital orifice
P penis
Pa paramere
Pr IX process of the ninth tergite
VIII, IX eighth and ninth sternite or tergite respectively

4. Righting Movements

The righting movements of the female imagines are similar to those of the larvae, though the sequence of resort to the two possibilities is not so strictly observed.

In Phausis males righting movement b) of the larvae and females is completely wanting; it probably could not be executed because of the wings and/or elytra and because of the short abdomen. The abdomen of Lampyris males is longer than the elytra, so that they can also execute righting movement b).

Movements a) and b) are made in rapid succession in the righting reflex of the males, a) always preceding.

F. Summary

Ecology, developmental cycle, larval biology, and sexual biology of the native lampyridae Lampyris noctiluca and Phausis splendidula were studied in the field and in the laboratory. The following findings may be presented:

1. Lampyris and Phausis as a rule have common biotopes. The typical biotope is damp, with well developed herb and brushwood strata. Their habitat is the ground stratum exclusively.

Sharp reactions to specific ecological factors (soil, humidity, brightness, temperature, etc.) and to their interaction and interplay keep the larvae in an environment whose microclimate exhibits the least possible fluctuations.

2. The cycle of development of both species is a three-year one. Complete individual data are available only for Lampyris, for which growing from eggs was successful in two stages; information on Phausis is limited to the first and last periods of life.

3. The larvae of both species have a seasonal cycle of activity in which a winter diapause (for Lampyris partial and facultative, for Phausis total and obligatory) alternates with an active period during the rest of the year.

4. The diurnal variation in activity (active by night, inactive by day) is accompanied by a rhythm of luminescence (erratic luminescence at night).

a) The rhythm of activity in Lampyris is strongly endogenously fixed. With other conditions constant it is only modifiable exogenously by change in illumination. Phausis adapts itself immediately to any change of phase in the variation of light.

b) The rhythm of luminescence obeys inherent factors, so that luminescence normally remains confined to the nocturnal active phase. The larvae do not glow continuously.

5. The chief food of the larvae in the open consists of shell-less and shelled snails. In captivity they accept animals of similar consistency (earthworms), and also fresh, wounded animal cadavers of the most varied groups.

6. The predatory behavior of both species of larvae differs from the practices of other snail specialists among the beetles and is markedly adapted to the habits of life of

the snails. The individual members of the typical stimulus-reaction chain between snail and larva need not follow each other rigidly, but may be repeated or skipped depending on the situation.

a) The larvae find the snails only by the trail of slime, which they follow closely, not by remote-perception senses. A snail slime trail can still be followed after 1 to 2 days. In this only the feelers of the first maxilla function as presumably olfactory sense organs.

b) For finding the fore end of the snail, which is important for the poison injection, neither optical nor tactile stimuli of the snail are decisive (Vogel [129] notwithstanding), but the differing (chemical?) composition of the slime at the fore and rear ends.

c) Disappearance of the fore end of the snail into the shell or under a dummy and also the absence of slime then bring about mounting the snail shell and "riding" on it.

d) The poison injected into the prey during the attack of the larva has an irreversible paralytic effect on all its movements; the paralysis presumably starts from the nerve centers in the fore end of the snail. The place where the poison is produced is undetermined; extracts from the most varied parts of the larva have a lethal effect on snails. The place of storage and concentration of the poison should not be sought in the intestine (Fabre [40], Vogel [127,129, 131]), but in the head of the larva. The stock of poison is exhausted after a few bites.

e) Positive thigmotaxis finally leads to carrying the prey away to a hiding place.

f) Extraintestinal digestion (Fabre [40], Vogel [127, 129, 131]) hardly appears to occur along with the normal intake of nourishment in the form of finely chopped food. The morphological structure of the biting mouth parts and of the pharynx provide for a normal intake of nourishment and appear well adapted to the snail diet.

7. The typical day-night rhythm of activity and luminescence which determines the sexual appetency behavior, the flight of the males, the waiting-and-glowing posture of the females, and the mating were observed and closely studied in the field and in the laboratory. This whole complex of behavior is astonishingly similar in the two species.

8. Experiments yielded the following results:

a) Daily cycle of activity and luminescence of the

imagines: The activity of both sexes and the (continuous) luminescence of the females are coupled, and normally fall in the night hours before midnight. Their duration is endogenously fixed, but the beginning can be induced by certain conditions of light. The other environmental conditions prevailing at the same time in the open (temperature, atmospheric humidity, wind, rain, and so on) have no effect.

b) Precipitating stimuli for the sexual behavior in the narrower sense: The sole effective stimulus for the flight of the males leading to coitus is the female light (remote stimulus). The female odor comes into play for the first time in the orientation of the male upon the female and only intensifies the further male sexual behavior after the approach flight has succeeded.

Tactile stimuli of the male then induce certain movements of the female. These movements in turn are important to the success of the copulation, but still copulation occurs even with dead females in the normal walking posture.

When isolated from the other components the whole shape of the female body and the shape of parts of it are not to be credited with any excitatory effect.

Dead or narcotized males produce no reactions in the females, and the light of the Phausis males is also ineffective.

c) The properties of the light of lampyridae: Spectral range (500-650 mμ), energy distribution of the spectral light and its maximum (550-580 mμ), and light intensity are the same in the two species and all developmental stages.

d) Luminous decoy experiments: Female decoys (= decoys with true-to-life female luminous surface patterns of the species in question) lighted with yellow light (= maximum of the spectral energy of the normal female light) evoke a maximum of approaches of the males of both species. This maximum is exceeded in the case of Phausis by another maximum located in the blue range of the spectrum, which does not occur at all in the emission spectrum of that species. Lampyris males do not react to blue, green, and red light, although they perceive it. Phausis males react well to all wave-lengths of visible light.

Phausis prefers female decoys of more than normal brightness, while Lampyris reacts maximally to the female light intensity.

Moving or rhythmically flashing female light decoys lessen the number of approaches in both species.

Oversized and undersized female light decoys reduce the number of approaches in the case of Lampyris, but in Phausis oversized ones have a more powerful effect.

Lampyris males in the natural habitat do not confuse the simultaneously glowing developmental stages of the two species, and especially the luminescing Phausis females, with females of their own species; Phausis males do confuse their own females with those of Lampyris.

Both unbroken and broken luminous surfaces produce a number of approaches that increases with their size, but only in the case of Phausis and not that of Lampyris do they equal the number of approaches to the normal female decoy. Broken surfaces have less attraction than unbroken ones.

The pattern of surfaces of the Lampyris female luminous organ is optimal for Lampyris males, and the degree of modification corresponds to the reduction in number of approaches. Any visible light works as a stimulus on Phausis. By schematization and multiplication of the elements of the Phausis female luminous organ it is possible to construct "supernormal" decoys, if their luminous surface is at the same time increased and glows with blue light.

Yellow-light decoys with a luminous pattern faithful to that of the Lampyris female luminous organ have a supernormal effect on Lampyris males (about 50% more approaches than to the glowing female).

e) From observations in the field and experiments with luminous decoys it appears that the Lampyris male finds his female by the arrangement of the luminous fields peculiar to the species and by the quality of the female light. Phausis males fly to all glowing surfaces of a certain size, color, and intensity, and find their females only by trial and error. Overproduction of males appears to compensate for this defect.

9. The eyes of the males deviate greatly from the usual morphological structure of superposition eyes, and so meet the demands made upon them, with respect to size, position on the head, 360° vision, binocular field of vision, great concentration of light and resolving power, to find their sexual partners. Their morphology exhibits no remarkable differences for the two species.

The eyes of the females of both species largely correspond to the usual structure of superposition eyes.

10. Lampyris males react positively to light intensities up to about 200 lx, and to greater intensities (at 1000 lx) indifferently or with definite negative phototaxis. In

Phausis males the change from positive to negative phototaxis occurs at 60 lx.

11. The sexual appetency behavior is disturbed in Lampyris females by light above 80 lx, in Phausis females by light above 100 lx.

12. Scototaxis (perception of form?) can be demonstrated only for the males, not the females.

Bibliography

*Cited in Harvey [55], Bioluminescence, New York, 1952.

*[1] Acloque, A. (1905), Le Ver Luisant (The Glowworm).

[2] Acloque, A. (1907), "The Light of the Insects," Le Cosmos (The Cosmos), Vol 56, pages 624-627.

*[3] Alexander, R.S. (1943), Factors Controlling Firefly Luminescence.

*[4] Anon, P.P. (1917), The Fireflies' Light.

[5] Autrum, H. (1951), "Excitatory Processes and Capacities of the Insect Eye," Verhandlungen der Deutschen Zoologischen Gesellschaft (Transactions of the German Zoological Society), 133-143.

[6] Bellesme, J. de (1871), "Observations on the Phosphorescence of the Eggs of Lampyris communis," Compte Rendu de l'Académie des Sciences (Proceedings of the Academy of Sciences), Paris, Vol 73, pages 629-630.

[7] Blunck, H. (1923), "The Development of Dityscus marginalis L. from Egg to Adult," part 2 (larval and pupal forms), Zeitschrift für die Wissenschaftliche Zoologie (Journal of Scientific Zoology), Vol 121, pages 171-391.

[8] Boettger, C.R. (1935), "The Land Snails' Defense Against Beetles," Sitzungsberichte der Gesellschaft Naturforschende Freunde (Minutes of the Society of Nature Research Friends), Berlin, 93-102.

*[9] Bongardt, J. (1903), Beiträge zur Kenntnis der Leuchtorgane Einheimischer Lampyriden (Contributions to Knowledge of the Luminous Organs of Native Lampyridae).

[10] Bongardt, J. (1904), "The Biology of Our Fireflies," Naturwissenschaftliche Wochenschrift (Natural Science Weekly), Vol 19, pages 305-310.

[11] Borchert, W. (1938), Die Verbreitung der Käfer Deutschlands (Distribution of the Beetles of Germany), Schönebeck.

[12] Bronn, H.G. (1928), Klassen und Ordnungen des Tierreichs (Classes and Orders of the Animal Kingdom), Vol 3, Mollusca, Section II, Gastropoda, Book 2, Pulmonata, Leipzig.

[13] Bronsart, H. von (1916), "The Problem of the Firefly," Entomologischer Rundschau (Entomological Review), Vol 33, pages 35-37 and 41-43.

*[14] Brown, D.E.S. and King, C.V. (1931), The Nature of Photo-

genic Response of Photuris pennsilvanica.

*[15] Buchner, P. (1914), Sind die Leuchtorgane Pilzorgane? (Are the Luminous Organs Fungus Organs?)

*[16] Buchner, P. (1922), Über das Tierische Leuchten (Animal Luminosity).

[17] Buchner, P. (1949), Symbiose der Tiere mit Pflanzlichen Mikroorganismen (Symbiosis of Animals with Vegetable Microorganisms), Berlin.

[18] Buchner, P. (1953), Endosymbiosis der Tiere mit Pflanzlichen Mikroorganismen (Endosymbiosis of Animals with Vegetable Microorganisms), Basel and Stuttgart.

*[19] Buck, J.B. (1935), Synchronous Flashing of Fireflies Experimentally Produced.

*[20] Buck, J.B. (1937), Studies on the Firefly: I. The Effects of Light and Other Agents on Flashing in Photinus pyralis with Special Reference to Periodicity and Diurnal Rhythm.

*[21] Buck, J.B. (1937), II. The Signal System and Color Vision in Photinus pyralis.

*[22] Buck, J.B. (1941), III. Spectrometric Data in Thirteen Jamaican Species.

*[23] Buck, J.B. (1948), The Anatomy and Physiology of the Light Organ in Fireflies.

[24] Buddenbrock, W. von (1952), Vergleichende Physiologie (Comparative Physiology), Vol I, Sinnesphysiologie (Sensory Physiology), Basel.

[25] Buddenbrock, W. von and Studnitz, G. von (1936), Vergleichend-Physiologisches Praktikum (Laboratory Manual of Comparative Physiology), Berlin.

*[26] Bugnion, E. (1919), Le Ver Luisant Provençal (Phausis delarouzeei Duval) (The Glowworm of Provence, etc.).

[27] Bünning, E. (1935), "On the Endonomic Diurnal Rhythm in Insects and in Plants," Berichte der Deutschen Botanischen Gesellschaft (Reports of the German Botanical Society), Vol 53, pages 594-623.

*[28] Carus, C. (1929), Über das Leuchten der Italienischen Leuchtkäfer (The Luminescence of Italian Fireflies).

*[29] Coblentz, W.W. (1911), The Colour of the Light Emitted by Lampyridae.

*[30] Conroy, J. (1882), The Spectrum of the Light Emitted by

the Glowworm.

*[31] Czepa, A. (1912), Organismenleuchten und Zweckmässigkeit (Luminescence of Organisms and Purposiveness).

[32] Czepa, A. (1912), "The Light of the Glowworm and Luminescence of Organisms in General," [illegible] (Monthly Journal of the Teaching of the Natural Sciences), Vol 5, pages 609-615.

[33] Demoll, R. (1918), Flug der Insekten und Vögel (Flight of Insects and Birds), Jena.

[34] Dieckhoff, L.A. (1842), "The Luminescence of the Lampyris Species," Stettiner Entomologische Zeitschrift (Stettin Entomological Journal), Vol 3, pages 117-119.

*[35] Dubois, R. (1887), De la Fonction Photogénique dans les Oeufs du Lampyre (The Photogenic Function in the Eggs of Lampyris).

[36] Edney, E.B. (1957), The Water Relations of Terrestrial Arthropods, Cambridge University Press.

*[37] Emery, C. (1884), Untersuchungen Über Luciola italica L. (Studies Concerning Luciola italica L.).

[38] Emery, C. (1887), "Light in the Love-Making of the Luciolae," [in Italian], Stettiner Entomologische Zeitschrift, Vol 48, pages 201-206; also in Bull. Soc. Entom. Ital. (Bulletin of the Italian Entomological Society), Vol 18, page 406 (1886).

[39] Exner, S. (1881), Physiologie der Facettierten Augen von Krebsen und Insekten (Physiology of the Faceted Eyes of Crustaceans and Insects), Leipzig, Vienna.

*[40] Fabre, H. (1914), The Glowworm, First User of Anaesthetics.

[41] Franz, V., "Glowworms in the Cold Season," Naturwissenschaftliche Wochenschrift, Vol 18, page 264 (1919), and Vol 19, page 80 (1920).

[42] Frömming, E. (1954), Biologie der Mitteleuropäischen Landgastropoden (Biology of the Terrestrial Gastropods of Central Europe), Berlin.

[43] Geiger, R. (1950), Klima der Bodennahen Luftschichten (Climate of the Strata of Air Near the Ground), Brunswick.

*[44] Geipel, E. (1915), Beiträge zur Anatomie der Leuchtorgane Tropischer Käfer (Contributions to the Anatomy of the Luminous Organs of Tropical Beetles).

*[45] Gerretsen, F.C. (1922), Einige Notizen über das Leuchten des Javanischen Leuchtkäfers Luciola Vittata Gast. (Some Notes on the Luminescence of the Javanese Firefly Luciola vittata Cast.).

[46] Geyer, D. (1909), Unsere Land- und Süsswasserschnecken (Our Land and Freshwater Mollusks), Stuttgart.

*[47] Goldschmidt, R.B. (1948), Glowworms and Evolution.

[48] Goldschmidt, R.B. (1951). "A Further Observation on 'Glowworms and Evolution,'" Die Naturwissenschaften (The Natural Sciences), Vol 38, pages 437-438.

*[49] Gorham, H.S. (1880), On the Structure of the Lampyridae with Reference to Their Phosphorescence.

[50] Gruner, H.E. (1954), Leuchtende Tiere (Luminescent Animals), in the series Die Neue Brehm-Bücherei, Wittenberg (Lutherstadt).

*[51] Haddon, K. (1915), On the Methods of Feeding and the Mouthpart of the Larva of the Glowworm (Lampyris noctiluca).

*[52] Harvey, E.N. (1929), Will the Adult Firefly Luminesce, If Its Larval Organs are Entirely Removed?

*[53] Harvey, E.N. (1940), Living Light.

*[54] Harvey, E.N. (1948), A General Survey of Bioluminescence.

[55] Harvey, E.N. (1952), Bioluminescence, Academic Press Inc., 649 St., New York.

*[56] Harvey, E.N. (1956),"Evolution and Bioluminescence," Quarterly Review of Biology, Vol 31.

*[57] Haupt, H. (1903), Leuchtende Organismen (Luminescent Organisms).

*[58] Hess, W.N. (1920), Notes on the Biology of Some Common Lampyridae.

[59] Hoffmann, R.W. (1925), "Periodic Diurnal Variation and Other Biological Rhythms in the Poikilothermic Animals," Handbuch Normaler und Pathologer Physiologie (Manual of Normal and Pathological Physiology), Vol 17, Corrol — III, pages 690 ff.

[60] Hoffmann, R.W., "Reflex Immobilisation States in the Animal Kingdom," ibidem.

[61] Holdhaus, K. (1929), "The Geographic Distribution of Insects," in Schröder's Handbuch der Entomologie (Manual of Entomology), Vol II, Jena.

*[62] Höllrigl, A.G. (1908), Lebensgeschichte von Lamprorhiza splendidula mit besonderer Berücksichtigung der Leuchtorgane (Life History of Lamprorhiza splendidula with Special Attention to the Luminous Organs).

[63] Hutson, J.C. and Austin, C.D. (1924), Notes on the Habits and Life History of the Indian Glowworm, Bulletin of the Department of Agriculture of Ceylon, 1-5.

[64] Ives, H.E. and Jordan, C.W. (1913), "The Intrinsic Brilliancy of the Glowworm," Scientific American, suppl., Vol 76, page 53.

*[65] Ives, H.E. and Jordan, C.W. (1922), The Firefly as an Illuminant.

[66] Jaeckel, S.H. (1953), Praktikum der Weichtierkunde (Laboratory Manual of Malacology), Jena.

[67] Jordan, K. (1910), "On 'Extraintestinal' Digestion in General and in Carabus auratus in Particular," Biologisches Zentralblatt (Central Journal of Biology), Vol 30, pages 85-96.

*[68] Knauer, F. (1910), Neues Über Unsere Leuchtkäfer (New Information About Our Fireflies).

*[69] Kölliker, A. von (1857), Über das Leuchten der Lampyris (On the Luminescence of the Lampyris).

*[70] Kuhnt, P. (1907), Das Leuchten der Lampyriden (The Luminescence of the Lampyridae).

[71] Leinemann, K. (1904), Über die Zahl der Facetten in den Zusammengesetzten Augen der Coleopteren (On the Number of Facets in the Compound Eyes of the Coleoptera), dissertation, Münster.

[72] Langerken, A. von (1924), "Extraintestinal Digestion," Biologisches Zentralblatt, Vol 44, pages 274-295.

[73] Loesser (1923), "The Luminescence of Animals," Die Umschau (Survey), Vol 27, pages 86-88.

[74] Lubbock, J. (1874), Origin and Metamorphoses of Insects, pages 17 ff., London.

*[75] Lund, E.J. (1911), On the Structure, Physiology, and Use of the Photogenic Organs, with Special Reference to the Lampyridae.

*[76] Macaire, J. (1821), Mémoire sur la Phosphorescence des Lampyres (Monograph on the Phosphorescence of the Lampyres).

[77] Magnus, G.F. (1954), "The Problem of Superoptimal Key

Stimuli," Verhandlungen der Deutschen Zoologischen Gesellschaft (Transactions of the German Zoological Society), Tübingen, pages 317-325.

*[78] Maille, A. (Mouen, A.A. de), Notes sur les Habitudes Naturelles des Larves de Lampyre (Notes on the Natural Habits of the Lampyris Larva).

[79] Main, H. and Priske, R.A.R. (1910-1911), "Notes of the Glowworm (Lampyris noctiluca)," Proceedings of the South London Entomological and Natural History Society, 74-76.

*[80] Main, H. and Priske, R.A.R. (1912), Glowworm Larvae Reared from Eggs.

[81] Mangold, E. (1920), "Animal Hypnosis," Ergebnisse der Physiologie (Findings of Physiology), Vol 18, pages 78-117.

*[82] Mast, S.O. (1912), Behavior of the Fireflies (Photinus pyralis?) with Special Reference to the Problem of Orientation.

*[83] McDermott, F.A. (1910), A Note on the Light Emission of Some American Lampyridae (I).

*[84] McDermott, F.A. (1911), Some Further Observations on the Light Emission of American Lampyridae: The Photogenic Function a Mating Adaption in the Photini (II).

*[85] McDermott, F.A. (1912), The Light Emission of the American Lampyridae: Notes and Correction on Former Papers (III).

*[86] McDermott, F.A. (1912), Observation on the Light Emission of American Lampyridae (IV).

*[87] McDermott, F.A. (1917), Observation on the Light Emission of American Lampyridae: The Photogenic Function as a Mating Adaption (V).

*[88] McDermott, F.A. (1914), Ecological Relations of Photogenic Function Among Insects.

[89] Meissner, O. (1907), Über das Schicksal der Männchen von Lampyris noctiluca (The Fate of the Males of Lampyris noctiluca), 24, page 140. [Name of journal omitted.]

*[90] Meissner, O. (1907), Wie Leuchten die Lampyriden? (How Do the Lampyridae Luminesce?)

[91] Meissner, O. (1908), "Growing Lampyris noctiluca Indoors," Monatshefte für Naturwissenschaftlichen Unterricht, Vol 1.

[92] Meissner, O. (1912), "On the Luminescence of the

Lampyridae," Coleopterologische Rundschau (Coleopterological Review), Vol 10.

*[93] Moore, J. (1908), Observations on Certain Organisms of a) Variations in Reaction to Light and b) a Diurnal Periodicity of Phosphorescence.

*[94] Morley, C. (1901), Notes on the Habits of Lampyris noctiluca L.

*[95] Newport, G. (1857), On the Natural History of the Glow-worm (Lampyris noctiluca).

[96] Olivier, E. (1909), "Organization of the Lampyridae," Comptes Rendu de l'Association Française pour l'Avancement des Sciences (Proceedings of the French Association for the Advancement of Science), Vol 37, pages 573-580.

[97] Olivier, E. (1910), "Contribution to the History of the Lampyres," First International Congress on Entomology, pages 273-282.

[98] Olivier, E. (1910), "Geographical Distribution of the Lampyridae," Comptes Rendu de l'Association Française pour l'Avancement des Sciences, Vol 38, pages 669-671.

[99] Olivier, E. (1910), "Lampyridae," in Coleopterorum Catalogus, Schenkling-Junk, Part 9, Berlin.

*[100] Owsjannikow, P. (1900), Ein Beitrag zur Kenntnis der Leuchtorgane von Lampyris noctiluca L. (A Contribution to Knowledge of the Luminous Organs of Lampyris noctiluca L.).

*[101] Parkins, M. (1931), Light of Glowworms.

[102] Petersen, A. (1912), "Contributions to the Comparative Physiology of the Digestion," Pflügers Archiv für die Physiologie (Pflüger's Archives of Physiology), Vol 145, pages 121 ff.

[103] Portillo, J. del (1936), "Relations Between the Angles of Aperture of the Ommatidia, the Curvature and Shape of the Insect Eye, and Their Functional Tasks," Zeitschrift für die Vergleichende Physiologie (Journal of Comparative Physiology), Vol 23, pages 100-145.

*[104] Pratje, A., Das Leuchten der Organismen (Luminescence of Organisms).

*[105] Prochnow, O. (1905), Lichtstärke von Lampyris noctiluca L. (Light Intensity of Lampyris noctiluca L.).

[106] Prochnow, O. (1921), "The Mechanics of Insect Flight," Schröder's Handbuch der Entomologie, (Manual of Entomo-

logy), No 7, pages 554-560.

[107] Pzibrams, H. and Megusar, F. (1912), "Measurements of Growth of Sphodramontia bioculata Burm.," Archiv für Entwicklungs-Mechanik (Archives of the Mechanics of Development), Vol 34, pages 680-741.

*[108] Ramdas, L.A. and Venkiteshwaran, L.P. (1934), The Spectrum of a Glowworm (Lampyridae).

*[109] Rau, P. (1932), Rhythmic Periodicity and Synchronism in Flashing in the Firefly Photinus pyralis with Notes on Photuris pennsilvanica.

[110] Recluz, M. (1829), "On the Habits of Lampyris noctiluca," Ann.Sc.obs.Raspail, Vol 2, page 299.

*[111] Rogerson, W. (1821), On the Glowworm.

[112] Rüschkamp, F. (1920), "On the Biology of the Drilidae and Micromaltidae," Biologisches Zentralblatt, Vol 40 pages 376-389.

[113] Schlieper, C. (1928), "The Distribution of Light Intensity in the Spectrum of Various Insects," Zeitschrift für die Vergleichende Physiologie, Vol 8, pages 261-286.

[114] Schmidt, R. (1939), Flug und Flieger im Pflanzen- und Tierreich (Flight and Fliers in the Plant and Animal Kingdoms), Berlin.

[115] Schneider, G. (1955), "The Spectral Sensitivity of the Receptor for 'Twilight Vision' in Calliphora," Zoologischer Anzeiger (Zoological Informer), Vol 18, pages 346-351.

*[116] Schulze, M. (1865), Zur Kenntnis der Leuchtorgane von Lampyris splendidula (The Luminous Organs of Lampyris splendidula).

*[117] Singh, P. and Manlik, S. (1910), Nature of Light Emitted by Fireflies.

[118] Skramlik, E.V. (1929), "Studies Concerning the Circulatory System in the Mollusks," Zeitschrift für die Vergleichende Physiologie, Vol 10, pages 1-19.

[119] Skramlik, E.V. (1941), "On the Circulation in the Mollusks," Ergebnisse der Biologie (Findings of Biology), Vol 18, pages 88-286.

[120] Snell, P.A. (1932), "The Control of Luminescence in the Male Lampyrid Firefly Photuris pennsylvanica with Special Reference to the Effect of Oxygen Tension on Flashing," Journal of Cellular and Comparative Physiology,

Vol 1, pages 37-51.

[121] Snyder, C.D. and ...l. (1920), "The Flashing Interval of Fireflies -- Its Temperature Coefficient," American Journal of Physiology, Vol 51, pages 536-543.

*[122] Spiller, J. (1882), Spectrum of the Light of the Glow-worm.

[123] Stellwaag, F. (1916), "How Do the Insects Steer During Flight?" Biologisches Zentralblatt, Vol 36, pages 30-44.

[124] Szymanski, J.S. (1920), "Motivity and Repose in Animals and Man," Zeitschrift für die allgemeine Physiologie (Journal of General Physiology), Vol 18, pages 165-182.

[125] Verhoeff, C. (1894), "Comparative Morphology of the Abdomen of Male and Female Lampyridae, Cantharidae, Malachidae, etc.," Archiv für die Naturgeschichte (Natural History Archives), Vol 60, I, pages 129-210.

*[126] Verhoeff, K.L. (1924), Zur Biologie der Lampyriden (On the Biology of the Lampyridae).

*[127] Vogel, R. (1912), Beiträge zur Anatomie und Biologie der Larve von Lampyris noctiluca L. (Contributions to the Anatomy and Biology of the Larva of Lampyris noctiluca).

*[128] Vogel, R. (1913), Zur Topographie und Entwicklungsgeschichte der Leuchtorgane von Lampyris noctiluca L. (On the Topography and Developmental History of the Luminous Organs of Lampyris noctiluca L.).

*[129] Vogel, R. (1915), Beitrag zur Kenntnis des Baues und der Lebensweise der Larve von Lampyris noctiluca L. (Contribution to the Knowledge of the Structure and Way of Life of the Larva of Lampyris noctiluca L.).

*[130] Vogel, R. (1922), Über die Topographie der Leuchtorgane von Phausis splendidula Lec. (On the Topography of the Luminous Organs of Phausis splendidula Lec.).

*[131] Vogel, R. (1927), Lampyrinae. Leuchtkäfer (Lampyrines. Fireflies).

[132] Vogel, R. (1929), "The Life of the Firefly Larva," Kosmos (Cosmos), Vol 26, pages 169-179.

[133] Voss, F. (1914), "Comparative Studies of the Organs of Flight of the Insects," Verhandlungen der Deutschen Zoologischen Gesellschaft, Vol 24-25, pages 59-90.

[134] Weber, H. (1954), Grundriss der Insektenkunde (Outline of Entomology), Stuttgart.

[135] Weber, L. (1909), "On the Firefly Phosphaenus hemipterus,"

Deutsche Entomologische Zeitschrift (German Journal of Entomology), pages 784-788.

[136] Weber, L. (1916-1917), "Vital Phenomena of the Beetles," Entomologische Blätter (Entomological Notes), Vol 13-14, Chapter IV: "The Luminous Organs."

*[137] Weitlaner, F. (1909), Etwas vom Johannes[illegible] (Lampyris splendidula and no[illegible]) ([illegible] Light of Fireflies (Lampyris splendidula and n[illegible])).

[138] Weitlaner, F. (1911), "More About the Light of Fireflies and Bioluminescence in General, with a Few General Reflections," Verhandlungen der Zoologisch-Botanischen Gesellschaft (Transactions of the Zoological and Botanical Society), Vol 61, pages 192-202.

*[139] Welsh, J.H. (1938), Diurnal Rhythms.

*[140] Wielowiejski, H. Ritter von (1882), Studien über die Lampyriden (Studies Concerning the Lampyridae).

[141] Willems, H.P.A. (1932), "On the Cardiac Motions in the Edible Snail (Helix pomatia L.)," Zeitschrift für die Vergleichende Physiologie, Vol 17, pages 1-100.

*[142] Young, C.A. (1870), The Spectrum of the Firefly.

[143] Zaunick, R. (1915), "The Biological Significance of the Slime of Snails," Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft (Newsletter of the German Malako-zoological Society), Vol 47, pages 34-41.

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