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SOME REMARKS ON THE OPTICS OF THE *BEMBEX*
ROSTRATA (L.) EYE (*HYMENOPTERA*, *SPHEGIDAE*)

by

JERZY ANDRZEJ CHMURZYŃSKI

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INTRODUCTION

Animal's senses take part in every manifestation of animal behaviour. We realize this particularly well now, in time of rapid development of cybernetics. The exteroceptors play an extremely important role in spatial orientation. Although there are indications that some animals take advantage of their proprioceptive impressions for orientation in space (cf. CHMURZYŃSKI, 1964; HERAN, 1958; MATTHEWS, 1955; MUNN, 1950; RABAUD, 1927), these are rarely predominant.

The studies of other authors on spatial orientation in female *Bembex rostrata* (L.), digger wasps of the family *Sphegidae*, have revealed unmistakably the predominance of eyesight in recognizing the way and place (BOUVIER, 1900, 1901; TINBERGEN, 1947). This has been reinforced by the author's own investigations (CHMURZYŃSKI, 1953, 1957, 1959, 1960). Thus, for a better estimation of the mechanics of spatial orientation, it proved necessary to know at least the fundamental facts concerning eyesight in this insect. The scanty data on eye structure in *Bembex rostrata* (L.) given by ZÄNKERT (1939) were not enough, and the information based on them could not be used to extrapolate the data on eyesight in bees (BAUMGARTNER, 1928; del PORTILLO, 1936; cf. CHMURZYŃSKI, 1964; HERAN, 1958).

Considering this, a preliminary study of the sight organ in *Bembex* was undertaken as part of a wider study on spatial orientation of this insect, which was the subject of the author's doctor's thesis (CHMURZYŃSKI, 1960).

METHOD

The analysis of the internal structure of the eye was done by the simplest technique: the material kept for a short time in 75% ethyl alcohol was then sectioned by means of a shaving blade. Both surfaces obtained from each section were photographed with a reflex camera under a binocular microscope using a $5\times$ objective and an Agfa "Isopan FF" film. Drawings, were made from $30\times$ enlargements of these photographs and from series of 5-10 drawings proper adjusted diagrammatic drawings were executed for each section.

The sections for analysis were made in the "frontal", "sagittal" and "horizontal" plane. Considering the objective of the study, which was spatial orientation of the insect, the planes were referred, unlike in PORTILLO's (1936) work, to the insect's body or head, not merely to its eyes (cf. Fig. 3).

The preliminary experiments on the critical flicker frequency were carried out in a 118-mm-radius stroboscope. The angular width of the bands was 4° .

RESULTS

Bembex, like many other predatory insects, has large compound eyes. These occupy the whole sides of the head with their fairly uniformly domed, oval, nearly bilaterally symmetrical surfaces, whose axes are in

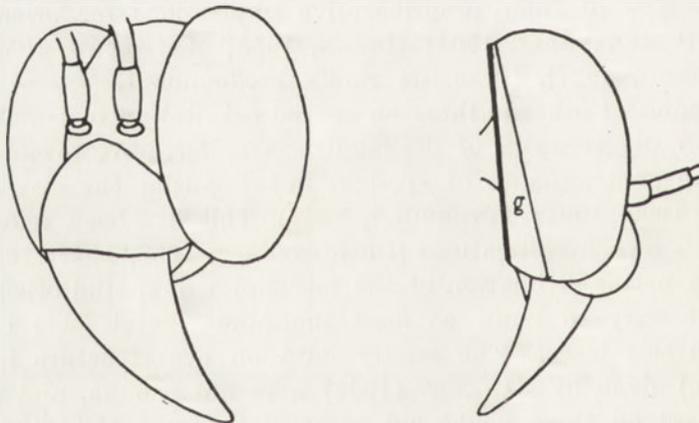


Fig. 1. Head of *Bembex rostrata* (L.) female on the scale of 10:1, a) in three-quarters, b) in profile, "g" — gena.

the ratio 1:1.5 (cf. Fig. 1 a). The eyes markedly project beyond the rest of the face. The long axes of the eyes are inclined at ca 10° to the frontal plane of the head, so that the genae — "g" in fig. 1 b — remain only in the lower postero-lateral part of the head. The inner boundary

of the eyes slightly curves archwise towards the frontal portion (Fig. 7), whilst the outer one nearly coincides with the occipital portion of the head (diverging from it downwards by about 10°). The radii of curvature in the medial portion of the arc in the sagittal, frontal and horizontal sections (Fig. 2) are in the ratio 2.2 : 1.5 : 1 respectively, which slightly

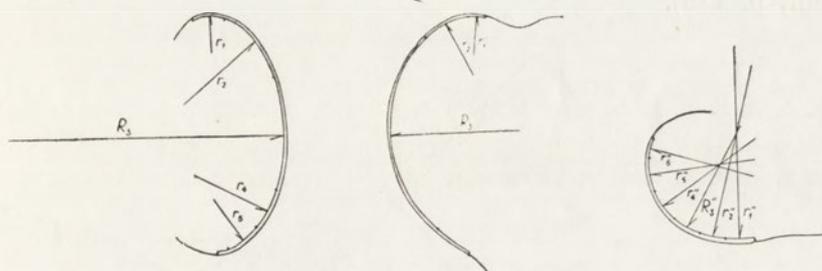


Fig. 2. Outline of external boundaries of a facet eye of a *Bembex rostrata* (L.) female on the scale of 10 : 1, a) in a sagittal section, b) in a frontal section, c) in a horizontal section. On the contours, segments have been distinguished constituting approximately arcs of circumferences of circles; the arrows mark the radii of their curvatures. "R₃", "R₃'" and "R₃''" indicate the radii referred to on p. 3.

departs from the corresponding relations in the bee: 2.5 : 2.2 : 1 (BAUMGÄRTNER, 1928¹; DEL PORTILLO, 1936, p. 114).

The eye of *Bembex rostrata* (L.), like that of other *Hymenoptera*, belongs to GRENACHER'S (1879) eucon structural type. The ommatides, whose number in one eye was found by ZÄNKERT (1939) to be 10 690, contain, according to this author, under a thick layer of corneolinsa four crystalline cones (coni cristallini) together with their cells surrounded by two primary iris cells coloured dark brown, 8 rosette-wise



Fig. 3. Horizontal (*h*) and frontal (*f*) section through a compound eye of a *Bembex rostrata* (L.) female with the lines along which the sections were made: *S'* — sagittal, *F* — frontal and *H* — horizontal section; *S* corresponds to the sagittal plane of a bee's eye in del PORTILLO's work (1936, fig. 9). Scale 10:1.

¹ The ratio of the radius of curvature of the transverse section to that of the horizontal one has been calculated from Figs. 25 and 26 in BAUMGÄRTNER's work (1928).

arranged visual cells with 12-18 secondary iris cells and, finally, a layer of dark violet-brown pigment of the retinula. The latter is most densely distributed on the membrana basalis, but in the ventral and dorsal region of the eye reaches nearly to the apexes of the crystalline cones, and in the central portion of the retinula is replaced by yellow iris pigment (*ibidem*, p. 116).

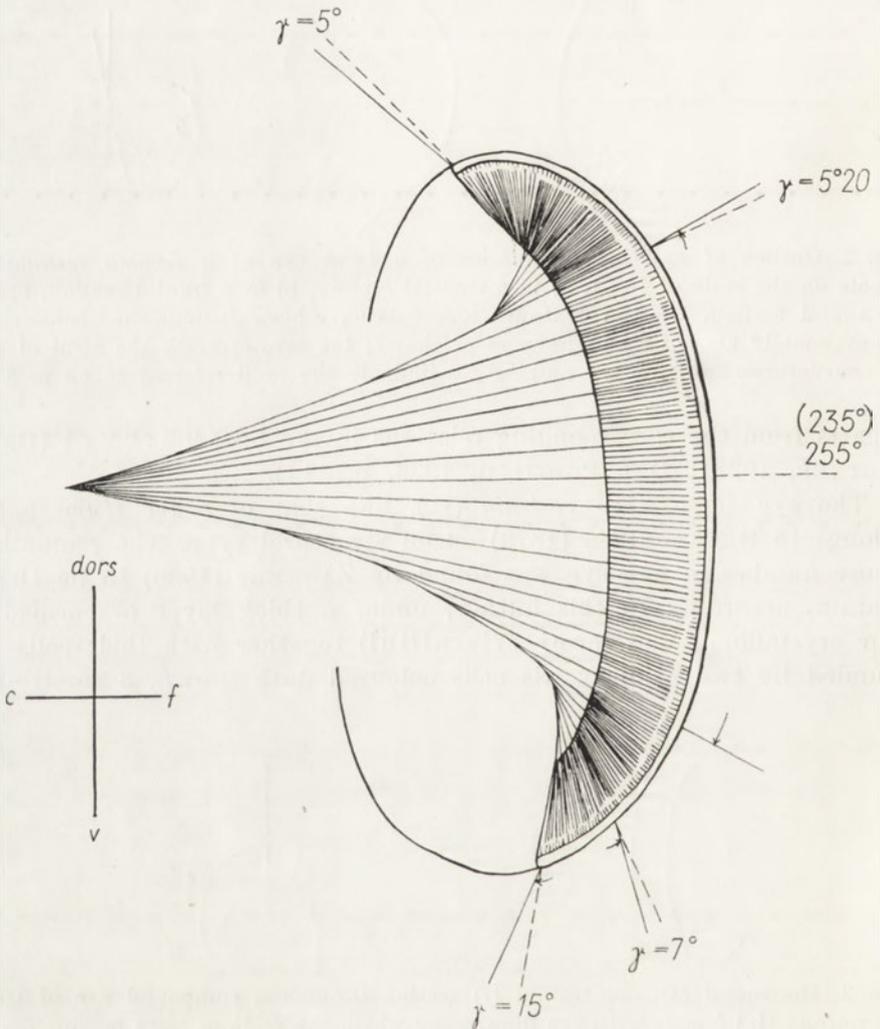


Fig. 4. Sections of a compound eye of a *Bembex rostrata* (L.) female shown in Fig. 3 a) sagittal section, b) frontal section, c) horizontal section — scale 30 : 1. The axis of every fifth rhabdom has been prolonged to show the differences in divergency of the ommatides. The continuous line indicates the boundaries of the visual field, the broken line — the rhabdom axes of the extreme ommatides; the corresponding angles are given. The remaining explanations in text.

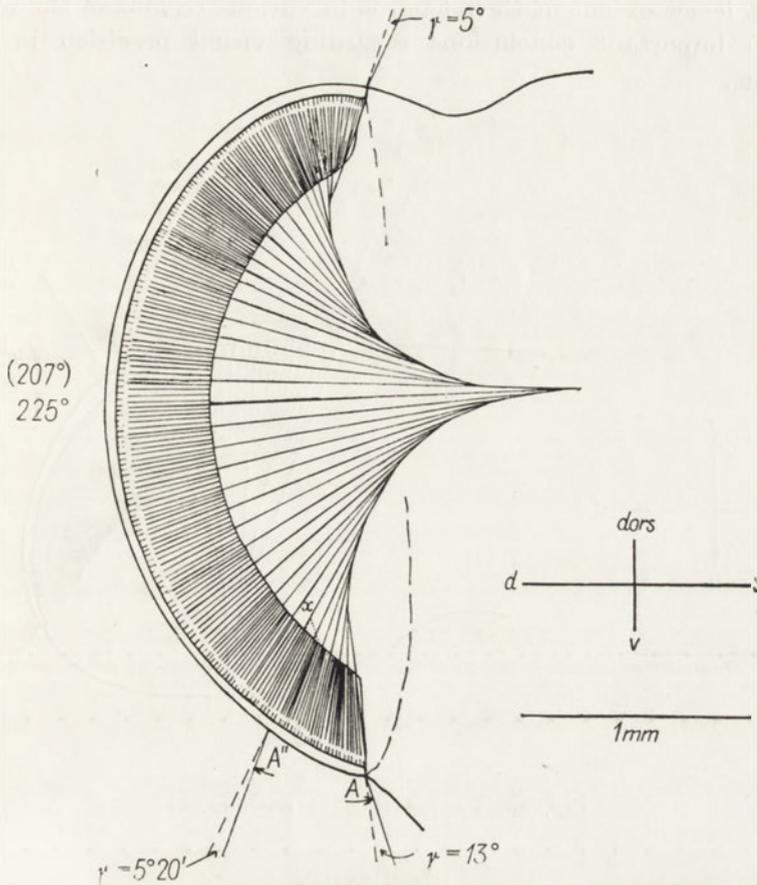


Fig. 4b. Explanation — see Fig. 4a.

The drawings (Fig. 4) of the frontal (*a*), sagittal (*b*) and horizontal (*c*) section point to a heterogeneous structure of the eye. The shape of the curves of intersection of the optical axes of the ommatides (every 5th axis is marked in the drawings) indicates in the first place an unequal angular separation of the rhabdoms. The smallest angles are formed by the anteriorly directed ommatides (Fig. 4 *c*) and those situated close to the "equator" of the eye (Fig. 4 *a*, *b*). From a comparison of Figs. 4 *b* and *c* it also follows that in the aforesaid portions of the sections the angles in the sagittal plane are smaller than those in the horizontal plane: their ratio in the sectors with minimum angles is ca 1 : 2; in the peripheral regions this ratio decreases to ca 1 : 1.3. Another outstanding feature is the variation of the diameters of the ommatides (working apertures)

and to a lesser extent of their lengths in various regions of the eye. This leads to important conclusions regarding visual precision in various directions.

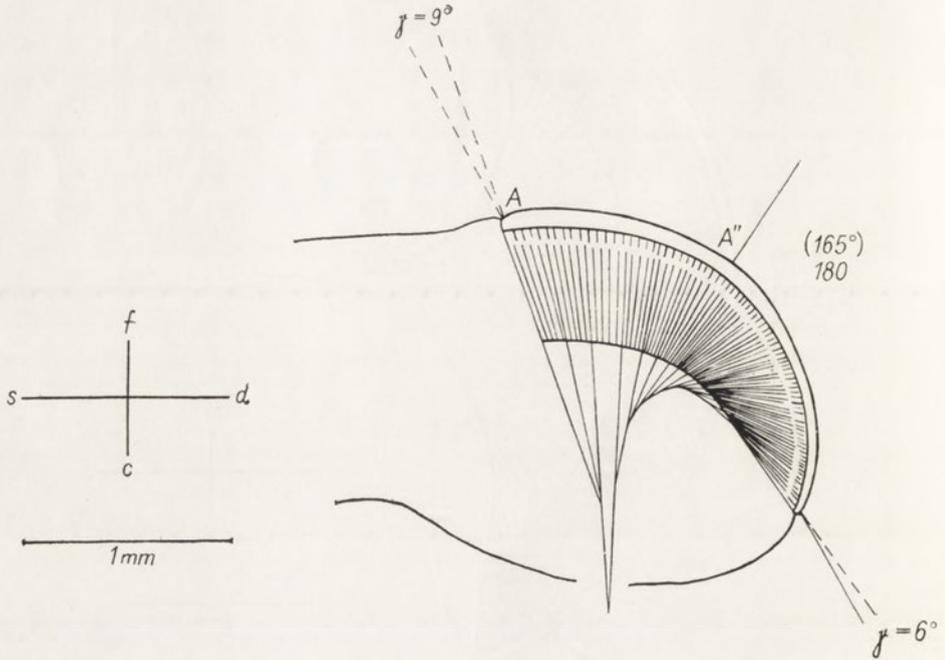


Fig. 4c. Explanation — see Fig. 4a.

DISCUSSION

As it was found already in the end of the XIX c., the apposition eye gives on the retinula a direct mosaic image of the object viewed. Each constituent ommatide, owing to its dioptric properties, reacts to rays entering it along its optical axis or at a small angle to it (MÜLLER, 1826; EXNER 1891; cf. BARLOW, 1952, p. 667; DETHIER, 1953, pp. 504-512; MAZOKHIN-PORSHNYAKOV, 1958). When, however, the optical axis of the corneal lens (*C-L* in Fig. 5) does not coincide with that of the crystalline cone (*C*) and of the rhabdom (*R*), then, as it follows from the formula $\sin \alpha = n \cdot \sin \beta$ — the refraction coefficient (n) of the corneal lens being known to differ from naught ($n = 1.52$ after BAUMGÄRTNER, 1928, p. 115) — in order to hit the light sensitive rhabdom, the light ray must fall after refraction (by angle β) so as to deflect from the optical axis of the corneal lens by $\sphericalangle \alpha > \sphericalangle \beta^1$. $\sphericalangle \alpha$ can be found by using the

¹ This is true of the insect in atmospheric medium.

above formula, the deflection angle of the axis of the corneal lens from that of the crystalline cone ($\alpha - \beta$) being known. Hence, from the equation $\gamma = \alpha - \beta$ we can find the deflection of the light ray from the rhabdom axis necessary for it to be perceived by the rhabdom after refraction in the corneolinsa. Angle γ , found by BAUMGÄRTNER (1928) for the bee's eye,

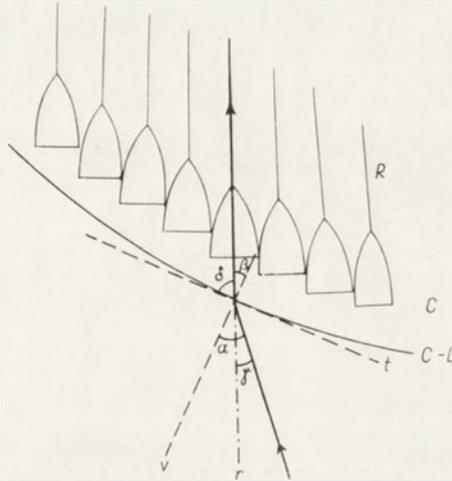


Fig. 5. Deflection of light ray perceived by an insect compound eye due to the fact that the optical axis of corneolinsa (C-L) and that of the rhabdom (R) do not coincide. C-conus cristallinus. Light ray inducing impression in the rhabdom marked with thick line. Subsidiary lines — broken: *t* — line tangent to corneolinsa, *v* — line perpendicular to it, *r* — prolongation of optic axis of conus cristallinus and the rhabdom.

in the eye of *Bembex* has been found to be largest for the peripheral ommatides, like in the bee. This of course affects the field of vision of the eye, extending it sideways, while slightly deteriorating the minimum separabile of the periphery of the eye, and increasing instead the working aperture of the lateral ommatides. This has been shown in Figs. 2, 6-8, 11 and 12. Thus, disregarding this correction, the visual field of the female *Bembex rostrata* (L.) has been found in the present study to be as follows: in the frontal plane 207° (from -97° below the horizontal plane to $+110^\circ$ above it), sagittally 235° (in accordance with ZÄNKERT's measurements, 1939, p. 118) and horizontally 165° (from -55° outwardly of the sagittal plane to $+110^\circ$ inwardly of it); with $\alpha - \gamma$ taken into account the respective values are: 225° (from -110° to $+115^\circ$)², 255° and 180° (from -61° to $+119^\circ$).

² The visual field of both eyes is 300° horizontally, the "blind" angle at the back is 60° .



Fig. 6. *Bembex rostrata* (L.) approaching her hole. The figure shows the boundaries of the visual field in the insect's sagittal plane and the prolongations of the rhabdom axes of the extreme ommatides (cf. Fig. 4 a).

The data gathered up in the present work also provide information on another problem of great importance for visual orientation — binocular vision. ZÄNKERT (1939, p. 117) found in *Bembex* a field of binocular vision

extending horizontally over 35° . Such field is presented in Figs. 7 and 8. It follows from the aforecited figures that the field of binocular vision in *Bembex* extends ca 50° upwards (the angle of intersection of the axes of the crystalline cones of the inward ommatides = 40°) ca 40° downwards the respective angle between the axes of the rhabdoms = 14°), and ca 60°

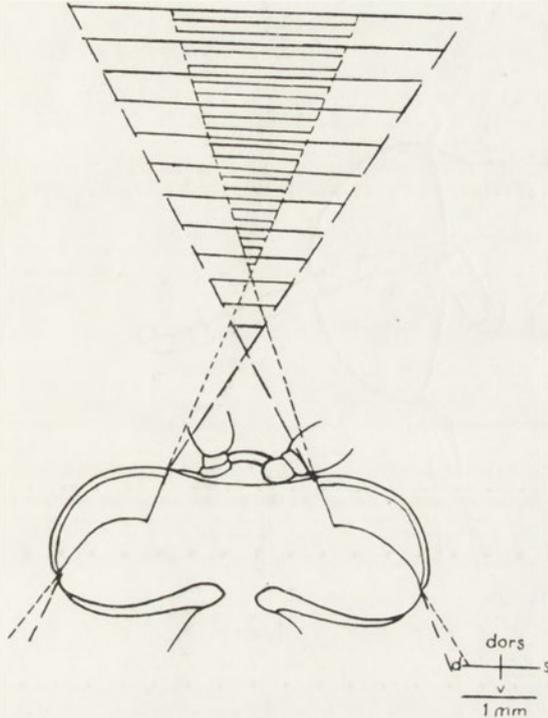


Fig. 7. Visual field of *Bembex rostrata* (L.) female in the horizontal plane on the scale of 10 : 1. The area of binocular vision is lined; more densely lined is the sector formed through intersection of the inner axes of the extreme rhabdoms. There are given the angles concerning the visual field and those within the extreme rhabdoms, all referring to the same compound eye (cf. Fig. 4 c).

forwards in the horizontal plane (the angle between the axes of the rhabdoms = 40° , which roughly corresponds to ZÄNKERT's 35° obtained by him probably by the same way).

The existence in *Bembex* of a zone of binocular vision makes it possible for this insect to estimate the distance — of course within the limits determined by the farthest and the nearest point perceived simultaneously with both eyes. This ability is of great significance for the insect, e. g. while preying; it also enables the male to keep a characteristic constant distance in his flight after the female. What are the limits within which the insect is able to estimate distance?

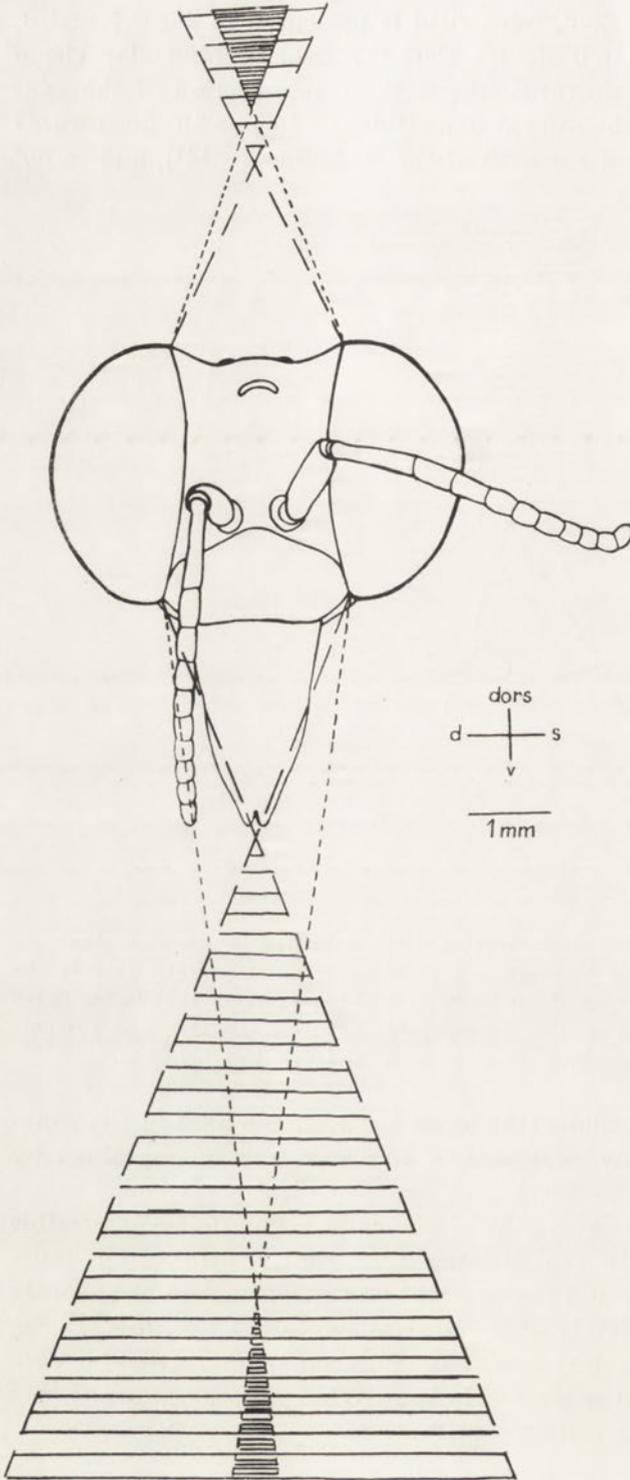


Fig. 8. Visual field of *Bembex* in the frontal plane on the scale of 10:1. For legend see fig. 7. (cf. Fig 4b).

Let us first find the nearest distance of binocular vision in the frontal plane downwards. In Fig. 9 a this is represented by segment OC . From the formula

$$OC = \frac{AO}{\operatorname{tg} \frac{\alpha}{2}}$$

with $AO = \frac{1}{2} AB = \frac{1}{2} \cdot 2.28 \text{ mm} = 1.14 \text{ mm}$, and $\alpha = 40^\circ$,

it follows that $OC = \frac{1.14 \text{ mm}}{\operatorname{tg} 20^\circ} = \frac{1.14 \text{ mm}}{0.3640} = 3.16 \text{ mm}$;

(correspondingly, the intersection point of the axes of the inner rhabdoms is 9.28 mm).

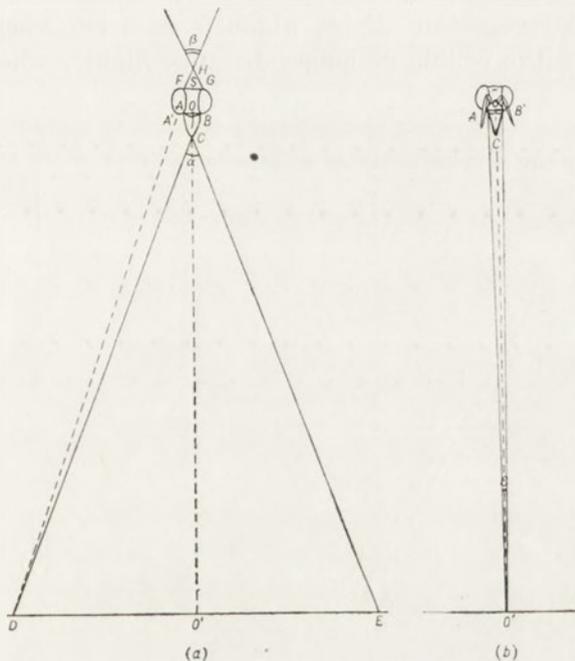


Fig. 9. Sketches for the analysis of binocular vision in *Bembex* in the frontal plane, scale 10:1 (cf. Fig. 8).

Point H , as follows from calculation, is at 2.47 mm distance from axis FG (the intersection point of the axes of the inner rhabdoms — 3.16 mm). This is the nearest distance of binocular vision in the frontal plane upwards.

In finding the distal limit of distance estimate in the same plane downwards we shall use Fig. 9 b.

An analysis of the sections of the eye shows that the angles of the ommatide axes running at a minimum angle to the ommatide axes running parallel for both eyes are ca 1° each (our simplified method of making diagrammatic drawings of sections of the eye makes greater accuracy impossible). The maximum limit of downward distance estimate, OO' , — when $\sphericalangle \varepsilon$ is determined at 2° and the distance between the ommatides ($A'B'$) is ca 2.3 mm — is about 66 mm.

Let us now find the range of binocular vision horizontally forwards; this is equally important from the point of view of *Bembex* ethology.

The proximal limit, in Fig. 10 a segment OC — when $AB = 1.72$ mm, $\sphericalangle a = 60^\circ$ — is 1.5 mm (while the intersection point of the axes of the inner rhabdoms is 2.36 mm). The distal one — in Fig. 10 b segment OO' — when $A'B' \cong 2.9$ mm, and $\sphericalangle \varepsilon = 2^\circ$ — is 80 mm.

The result is in keeping with the most frequent ceiling of *Bembex* orientation and recognition flight, which is ca 5 cm when slow (1.5-2.5 m/sec) and with the ceiling of longer-distance flights, when *Bembex* flies

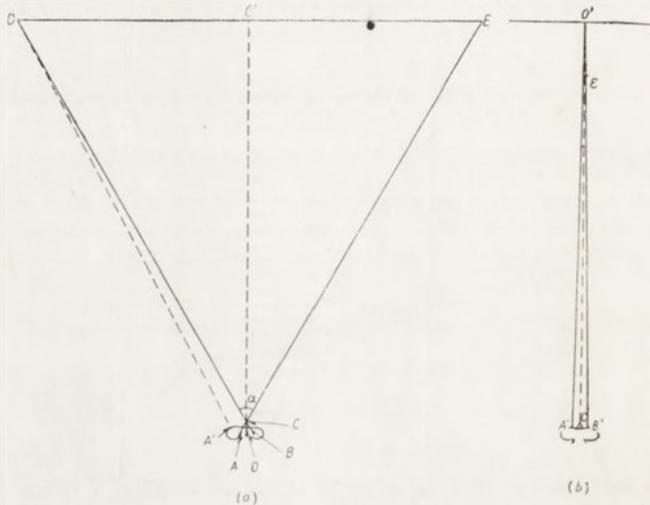


Fig. 10. Sketches for the analysis of binocular vision in *Bembex* in the horizontal plane, scale 1 : 1 (cf. Fig. 7).

just above the grass tops, 5-50 cm above the ground, i. e. still within the scope of its capability of estimating height relative to the ground or to the grass tops.

To realize the role of sight in those situations, two other factors

are important to know: the extent of the binocular visual field at this maximum distance and the minimum separabile of the eye, particularly in this important sector.

To find the first one we shall use Fig. 9 a and 10 a. Its values will be found by calculating the lengths of segments *DE*.

Thus the width of the field of binocular vision in the frontal plane downwards (Fig. 9 a) at the far limit of distance estimate (when $OO' = 6.6$ mm, i. e. $CO' \cong 6.3$ cm; $\sphericalangle \alpha = 40^\circ$) is

$$2 \cdot DO' = 2 \cdot CO' \operatorname{tg} \frac{\alpha}{2} = 2 \cdot 6.6 \text{ cm} \cdot 0.3640 \cong 4.8 \text{ cm};$$

horizontally forwards (Fig. 10 a) (when $CO' \cong OO' \cong 8$ cm; $\sphericalangle \alpha = 60^\circ$):

$$DE = 2 \cdot DO' = 2 \cdot CO' \operatorname{tg} \frac{\alpha}{2} = 2 \cdot 8 \text{ cm} \cdot 0.5774 \cong 9.2 \text{ cm}.$$

By applying cautious interpolation it may be presumed that at the moment of reaching the nest, i. e. in a direction inclined at roughly 45° downwards from the horizontal plane, the width of the field of binocular vision at a distance of ca 7 cm is ca 8 cm.

The next item to consider is the minimum separabile of the eye of the female *Bembex rostrata* (L.).

First some concepts important for further considerations must be established.

What is termed "visual field" ("Gesichtsfeld"; "campus visualis" — TCHERMAK, 1931) is the angle (ω) between two straight lines along which run the marginal rays for a given eye section hitting the light-sensitive elements (in a compound eye: rhabdoms); cf. Fig. 4, 6, 7 and 8. The "visual angle" ("Gesichtswinkel"; "angulus visualis"³) (α) — generally smaller than ω — is the angle formed by two straight lines drawn to the eye from two extreme points of the object viewed.

The smallest visual angle at which the eye can still distinguish both extreme points is called the minimum separabile of the eye (\varnothing). A very significant quantity is $\operatorname{tg} \varnothing$, for it represents the maximum distance (l_{\max}), from which the eye can distinguish two points spaced in a plane perpendicular to the eye's visual direction, viz.

$$l_{\max} = \frac{\alpha}{\operatorname{tg} \varnothing}$$

³ Those definitions concerning objective space have after TCHERMAK (1931, p. 837) subjective counterparts: "Sehfeld" ("campus opticus") and "Sehwinkel" ("angulus opticus").

and the minimum space (a_{\min}) between two points distinguishable from distance l :

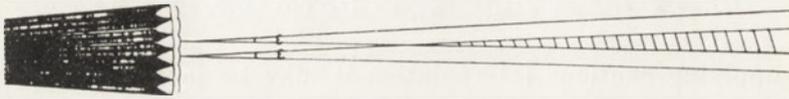
$$a_{\min} = l \cdot \operatorname{tg} \varnothing. \quad (1)$$

With these concepts is closely connected the resolving power ("Auflösungsvermögen"⁴ (R) defined after HECHT (1934) by the formula:

$$R = \frac{1}{\varnothing}; \quad (2)$$

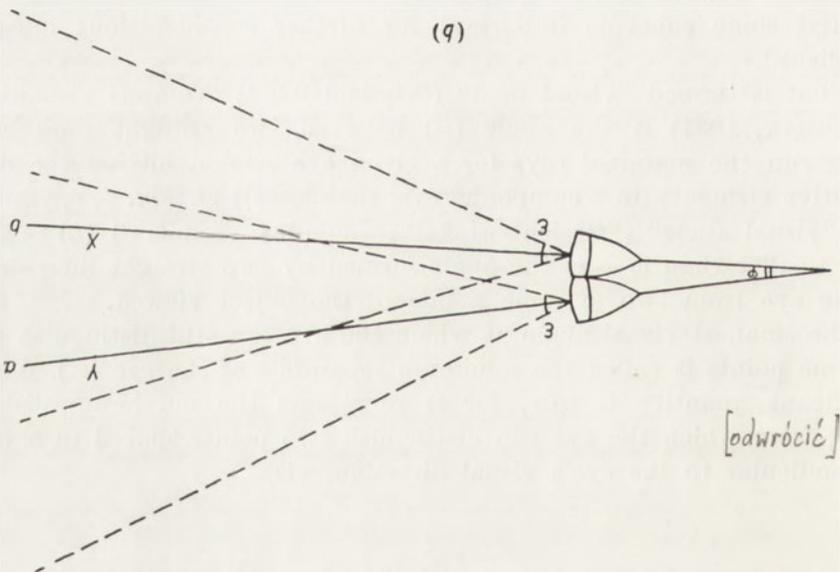
The unit accepted for it is the value R at $\varnothing = 1'$ (resolving power of human eye).

(In literature concerned with the physiology of eye-sight in insects, e. g. von BUDDENBROCK, 1952, pp. 147-148, 151; DETHIER, 1953, pp.



(a)

Fig. 11 a. Diagrammatic drawing showing overlapping of visual fields of adjoining ommatides in apposition eye of an insect.



(q)

Fig. 11 b. Analysis of minimum separable of an insect's compound eye. Angles excessively obtuse for clarity of picture.

⁴ Sometimes these terms are found to denote the minimum separable.

504-512; MAZOKHIN-PORSHNYAKOV, p. 62, the resolving power is also called visual acuity ("Sehschärfe"). It is better, however, to reserve this term for the quantity determined by the following correlation (HEGNER, 1937, p. 478):

$$O = \frac{g}{l'}$$

where g — minimum distance from which the eye is able to perceive an object clearly, l' — distance at which the eye perceives a given object at angle \varnothing .

Until recently it was generally believed that the minimum separable of a compound eye roughly corresponded⁵ to the ommatidial angle ("Öffnungswinkel") (ψ)⁶. Such approach, however, is by no means satisfactory. Even if we assume, following a large number of workers (cf. p. 4), MÜLLER'S (1826) principle saying that the ommatide perceives rays slightly deflecting $\left(\frac{\varepsilon}{2}\right)$ from its optical axis, then (Fig. 12), provided the angular separation of the ommatides (φ) is not too large, the extreme inner rays perceived by these elements will intersect at some point (C); consequently, at a sufficiently long distance from the eye two points (x and y) lying exactly on the axes of those neighbouring ommatides (a and b) will be in the visual field of both eyes, and therefore will not be distinguished (cf. MAZOKHIN-PORSHNYAKOV, 1958, Fig. 1). In line with the above argumentation BARLOW (1954) states that the resolving power of a compound eye (\varnothing) is never smaller than double the angular separation of the ommatide axes (φ) also called the ommatide angle density (MAZOKHIN-PORSHNYAKOV, 1958)⁷;

⁵ AUTRUM (1952, p. 439), de VRIES (1956, pp. 246-248), de VRIES and KUIPER (1958, pp. 200-201) assume that the visual field of the ommatide becomes wider owing to light disruption on its small aperture.

⁶ It is equally incorrect to think that the ommatidial angle (ψ) is equal to the visual angle of the ommatide (ε) or to call it aperture. The numerical aperture of the ommatide is the quantity

$$A = n \cdot \sin \varepsilon;$$

in atmospheric medium, where $n = 1$, $A = \sin \varepsilon$.

In cases of a very small ommatidial angle, when $\sphericalangle \varepsilon \cong \sphericalangle \psi$, if the length of the ommatide is assumed to be 1, only

$$A \cong \delta,$$

where δ — diameter of the aperture of the ommatide.

⁷ As a matter of fact, these authors have in mind slightly different quantities, for according to BARLOW (1952) the angular separation of the ommatides

$$\varphi = \omega/N,$$

so

$$\varnothing = 2\varphi,^8$$

and since

$$\varphi = \psi,$$

hence

$$\varnothing = 2\varphi = 2\psi. \quad (6)$$

On the other hand, he demonstrated that \varnothing depended also on the resolving power of the ommatide (ϑ) defined by the formula for the telescope:

$$\vartheta = \frac{1.22\lambda}{\delta}, \quad (7)$$

(ϑ — in rad., δ — in cm), where λ is the wave-length of a given light, δ the diameter of the ommatide aperture. Optimum ϑ is ensured when

$$\vartheta > \psi \geq 0.4\vartheta; \quad (8)$$

it is best when ψ is not much smaller than ϑ . The minimum ommatidial angle guaranteeing good minimum separabile to the compound eye is

$$\psi_{\min} = \varphi_{\min} = 0.4\vartheta. \quad (9)$$

where ω — visual field, N — number of ommatides in $\sphericalangle \omega$, while the ommatide angle density in MAZOKHIN-PORSHNYAKOV'S (1958) sense:

$$\varphi = a/n, \quad (3)$$

where a — visual angle (generally $a < \omega$) and n — number of ommatides in $\sphericalangle a$; and it is a well-known fact that the diameters of the apertures of the ommatides (δ) linked to those quantities by the formulae:

$$d = n\delta \quad (4)$$

and

$$\varphi = \frac{\omega\delta}{d}, \quad (5)$$

(where d — row of ommatides in angle ω) are different in various sectors of the eye, as may be seen in *Bembex* (cf. p. 3, 4).

⁸ For reasons expressed in the footnote (7) on the preceding page, we should consider the minimum separabile of only a part of the eye more or less homogeneous in structure; this would be expressed by the formula

$$\varnothing_{\text{part}} = 2\varphi_{\text{part}}, \quad (4a)$$

where $\sphericalangle \varphi_{\text{part}}$ would be found according to MAZOKHIN-PORSHNYAKOV'S (1958) formula (3), and so

$$\varphi_{\text{part}} = \frac{a}{n}. \quad (3a)$$

From formulae (5), (7) and (9), it follows that the lower limit of utility of the ommatide diameter is determined by

$$\delta \geq \sqrt{\frac{0.49 \lambda d}{\omega}},$$

or

$$\delta_{\min} = \sqrt{\frac{0.49 \lambda d}{\omega}}; \quad (10)$$

hence the value of the minimum separabile of part of the compound eye is expressed by the formula:

$$\varnothing_{\text{part}} = 2\varphi_{\text{part}} = 2\psi_{\text{part}} = 2\sqrt{\frac{0.49 \lambda \omega}{d}} \quad (11)$$

(ω — in rad., d — in cm). In accordance with this formula BARLOW (1952) found the minimum separabile of the bee's eye to be $1^{\circ}56'25''$.

Of course, it must be borne in mind that besides depending on the structure of the dioptric apparatus, the minimum separabile of the eye is also affected to a certain degree by possible nervous connections between ommatides and by the sensitiveness of the rhabdoms⁹, and so the conclusions concerning the functioning of the eye drawn from its structure should be regarded as a more or less legitimate hypothesis.

After the above remarks we may now try to estimate the minimum separabile of some interesting sectors of the *Bembex* eye.

Let us first study the precision with which segments DE in Fig. 9 a and 10 a, lying in the binocular vision zone are perceived.

To find that we must know the number of rhabdoms stimulated by the rays running from that segment. From their number contained in arc $\widehat{AA''}$ angle φ may be found.

Let us assume with approximation that $\sphericalangle DA''E = \sphericalangle a$ (actually they differ by ca -1° for $\sphericalangle DA''E$; for simplicity, in this phase of calculations we disregard the fact that properly speaking the angle in question is $\sphericalangle DxE$, where x is the intersection point inside the eye of the straight lines EA and DA'' running to the ommatides which perceive them (cf. Fig. 4 b). The deflection of these lines from the axes of the rhabdoms must be taken into account.

If we assume that for Fig. 9 a and correspondingly for Fig. 4 b, it follows that the straight line DA'' running at $\sphericalangle 40^{\circ}$ to the straight line

⁹ It should be mentioned that de VRIES and KUIPER (1958) came to conclusion that rhabdoms did not work as a whole, but possibly as a bundle of independent light-sensitive elements, rhabdomers.

EA reaches the 27th ommatide starting from the inner side (for it $\sphericalangle \gamma = 5^\circ 20'$), i. e. the centre of the corneal lens is exactly point A'' . From formula (3 a) we obtain:

$$\varphi_{\text{part}} = \frac{40^\circ}{27} = 1^\circ 27',$$

and so the minimum separabile of this sector (40° of the inner visual angle vertically downwards in the frontal plane) is:

$$\varnothing_{\text{part}} = 2\varphi_{\text{part}} = 2 \cdot 1^\circ 27' = 2^\circ 54'.$$

From formula (1),

$$a_{\text{min}} = l \cdot \text{tg} \varnothing$$

(where a_{min} is the minimum linear distance distinguishable by the eye from distance l at the eye's minimum separabile \varnothing) in the case under consideration it follows that

$$a_{\text{min}} = 66 \text{ mm} \cdot \text{tg} 2^\circ 54' = 66 \text{ mm} \cdot 0.0507 = 3.7 \text{ mm}.$$

With the horizontal inner angle 60° , at which segment DE in Fig. 10 a (cf. Fig. 4 c) is seen by the eyes the respective values are:

$$\varphi_{\text{part}} = \frac{a}{n} = \frac{60^\circ}{29} = 2^\circ 04';$$

$$\varnothing_{\text{part}} = 2\varphi_{\text{part}} = 2 \cdot 2^\circ 04' = 4^\circ 08';$$

$$a_{\text{min}} = l \cdot \text{tg} \varnothing = 80 \text{ mm} \cdot \text{tg} 4^\circ 08' = 80 \text{ mm} \cdot 0.0722 = 5.8 \text{ mm}.$$

A segment perpendicular to DE at the same distance and at the same angle in the sagittal plane is seen by the *Bembex* eye with the following minimum separabile (cf. Fig. 4 a):

$$\varnothing_{\text{part}} = \varphi_{\text{part}} = 2 \cdot \frac{60^\circ}{82} = 2 \cdot 0.731^\circ = 1.462^\circ = 1^\circ 28';$$

whereas

$$a_{\text{min}} = l \cdot \text{tg} \varnothing = 80 \text{ mm} \cdot \text{tg} 1^\circ 28' = 80 \text{ mm} \cdot 0.0256 \cong 2 \text{ mm}.$$

(For comparison, minimum separabile in the same plane downwards — cf. fig. 4 a — is:

$$\varnothing_{\text{part}} = 2\varphi_{\text{part}} = 2 \cdot \frac{40^\circ}{20} = 2 \cdot 2^\circ = 4^\circ;$$

whereas

$$a_{\text{min}} = l \cdot \text{tg} \varnothing = 66 \text{ mm} \cdot \text{tg} 4^\circ = 66 \text{ mm} \cdot 0.0699 = 5.7 \text{ mm}.$$

The data obtained in the present study indicate that the *Bembex* female most probably shows a different resolving power (R) in various parts of her visual field and, in line with the first impression imparted by the eye sections, in various visual planes. The optimal resolving power, judging from the *Bembex* eye structure, is found along the prolonged axis of the body in the sagittal plane:

$$R_{\text{part}} = \frac{1}{\varnothing_{\text{part}}} = \frac{1}{1^{\circ}28'} = \frac{1}{88'} = 0.0114,$$

which is over twice its value in the same region in the horizontal plane:

$$R_{\text{part}} = \frac{1}{4^{\circ}08'} = \frac{1}{248'} = 0.0040.$$

Downwards the resolving power is nearly as poor in the sagittal plane

$$R_{\text{part}} = \frac{1}{4^{\circ}} = \frac{1}{240'} = 0.0040,$$

as in the frontal plane

$$R_{\text{part}} = \frac{1}{2^{\circ}54'} = \frac{1}{174'} = 0.0057.$$

Generally speaking, the resolving power in *Bembex rostrata* (L.) is probably 90 to 250 times lower than in man.

However, a statistical approach to the efficiency of the eye gives only a partial insight into the insect's ability of optical perception. It should be kept in mind that *Bembex* is a predatory insect flying fast and generally low. Now, perceiving moving objects sets special requirements before the visual analyser. It demands from the visual cells high contrast sensitiveness, and high critical flicker frequency (Verschmelzungsfrequenz) from the whole analyser. It may be presumed that these features in *Bembex* resemble those in the honey-bee, which perceives a stimulus occupying ca 24% of the visual field of the ommatide, i. e. an object whose angular measurement is 17'24" (VON BUDDENBROCK, 1935), while its maximal critical flicker frequency for one ommatide is 165/sec, and for a group of ommatides 300/sec (AUTRUM and STÖCKER, 1950). The preliminary attempts to evaluate the critical flicker frequency carried out on *Bembex rostrata* (L.) females by the optomotor method speak for the acceptance of the former quantity, 165/sec, and so it will be used as basis for further considerations.

Of course, the flicker frequency during flight is highest for the lateral and lower ommatides, in which the images succeed one another at the highest rate, and in this case a larger angular separation of the axes of

the ommatides creates better conditions for distinguishing the objects passed, the angle at which they are best distinguished being the larger the nearer the objects. Considering this, the heteromorphous structure of the *Bembex* eye is biologically most justified. To show the significance of those characteristics of the sight in *Bembex* in various vital situations, it is interesting to study the correlation between the height of the flight and its speed in the light of the foregoing considerations. Here are some facts:

(1) According to the author's yearly observations carried out for 12 years, an ordinary flight of *Bembex rostrata* (L.), e. g. from the nest to the feeding grounds, is generally performed at a steady slow (1.5-2.5 m/sec) or fast (3-6 m/sec) rate at a height of 5-50 cm; the most common height is ca 30 cm above ground; a lower flight generally belongs to the steady slow type.

(2) An expanded orientation flight, e. g. after a change of environment of the nest, is generally performed at a height of 2-15 cm at slow speed; a simple flight from the nest is performed at high speed, ca 3 m/sec, at a height of ca 20 cm.

(3) Similar characteristics are shown by the return to the nest — the recognition flight. A closer analysis of all types of flight is impossible both lack of space and for the insufficiency of the existing data on the functioning of the *Bembex* eyes. Let us then only consider what theoretical conclusions follow from the recorded values of velocity of flight — the mean velocity of slow-speed flight: 2 m/sec and the mean velocity of high-speed flight: 4.5 m/sec¹⁰.

The first principle of the insect's vision during flight is the correlation between its minimum separabile (\varnothing), its critical flicker frequency (ν), the density of the objects viewed (x — linear distance between them, ζ — angular distance between them, x_{\min} — smallest admissible distance between them corresponding to the minimum separabile — \varnothing) and the velocity of flight (v). It may be formulated as follows:

$$x = \frac{v}{\nu} = h \cdot 2 \operatorname{tg} \frac{\zeta}{2}, \quad (12)$$

and for small $\ast \zeta$:

$$x \cong h \cdot \operatorname{tg} \zeta$$

(where h — ceiling of flight, and $\ast \zeta \geq \ast \varnothing$) and

$$x_{\min} \cong h \cdot \operatorname{tg} \varnothing. \quad (13)$$

¹⁰ The velocity of flight given by NIELSEN (1945, p. 37) for *Bembex rostrata* — 8 m/sec — lies within the range of its maximum capacity, the so-called by the author "lightning flight" (the author observed up to 9 m/sec).

The foregoing formulae will be now applied for an evaluation of the visual capability of *Bembex* during slow-speed orientation flight at a height of 15 cm and during high-speed flight at a height of 30 cm.

(1) What is the maximal velocity at which *Bembex* may fly at a height of 15 cm to be able to distinguish details of the ground separated by $\times \varnothing$ from each other, i. e.

$$x_{\min} \cong h \cdot \operatorname{tg} \varnothing = 15 \text{ cm} \cdot \operatorname{tg} 4^\circ = 15 \text{ cm} \cdot 0.0699 = 1.05 \text{ cm} ?$$

From a conversion of formula (12) we obtain

$$v_{\max} = v \cdot x,$$

from which, after substituting the above-mentioned values, we obtain the answer:

$$v_{\max} = 165/\text{sec} \cdot 1.05 \text{ cm} = 1.7 \text{ m/sec},$$

i. e. within the limits of low-speed flight, not too far from the mean, velocity $v = 2 \text{ m/sec}$.

(2) What is the minimum height at which *Bembex* may fly at a velocity of 4.5 m/sec to be able to distinguish details of the ground separated by $\times \varnothing$ from each other?

The answer is:

$$h_{\min} = \frac{v}{v \cdot \operatorname{tg} \varnothing} = \frac{4.5 \text{ m/sec}}{165/\text{sec} \cdot 0.0699} = 39 \text{ cm}.$$

The values thus obtained are in fairly good keeping with the observation data. It may then be presumed that the assumptions on which has been based the evaluation of the visual capability of *Bembex* are fundamentally right. On the other hand it should be stated that the resolving power of the *Bembex* eye calculated on the base of the aforesaid assumptions at velocities of flight characteristic of this insect ensures an adequate precision of vision, so that eye-sight may constitute the basic element in its spatial orientation.

SUMMARY

The present work is concerned with a preliminary evaluation of the optical properties of the compound eyes in *Bembex rostrata* (L.) (*Hymenoptera—Aculeata, Sphegidae*) females on account of their capability to return to the nest, which is generally situated in sandy soil grown with thin gramineous vegetation.

The analysis of the internal structure of the eyes was based on drawings of frontal, sagittal and horizontal sections made from a series of photographs of these sections taken on material fixed in ethanol.

The structure of the eye has been found to be heterogeneous. The smallest angles are formed by ommatides directed forwards and by those situated near the "equator" of the eye. In these parts of the sections the angles in the sagittal plane are smaller than those in the horizontal plane: their ratio for the sectors with minimum angles is ca 1 : 2.

The visual field of the *Bembex rostrata* (L.) female ^{eye} covers $\times 207^\circ$ in the frontal plane, $\times 235^\circ$ in the sagittal plane, and $\times 165^\circ$ in the horizontal plane.

The field of binocular vision covers in the frontal plane upwards $\times 50^\circ$, downwards $\times 40^\circ$, in the horizontal plane forwards $\times 60^\circ$.

It follows from calculations that an estimation of distance is possible downwards within the range of 3-66 mm, horizontally forwards between 1.5 and 80 mm. The minimum separabile is theoretically in the downward direction: in the frontal plane $2^\circ 54'$, and in the sagittal plane 4° ; in the forward direction: in the horizontal plane $4^\circ 08'$, and in the sagittal plane $1^\circ 28'$.

At a critical flicker frequency evaluated in the preliminary experiments at ca 165/sec, the insect has a theoretical capability of adequately distinguishing details of the ground while flying at a speed of 1.7 m/sec at a height of 15 cm, or at a speed of 4.5 m/sec at a height of 39 cm. These values are very close to those observed under natural conditions.

SPOSTRZEŻENIA NAD WŁASNOŚCIAMI OPTYCZNYMI OCZU ZŁOŻONYCH U *BEMBEX ROSTRATA* (L.) (*HYMENOPTERA*, *SPHEGIDAE*)

STRESZCZENIE

Celem niniejszej pracy jest wstępna ocena własności optycznych oczu złożonych samic *Bembex rostrata* (L.) (*Hymenoptera-Aculeata*, *Sphegidae*) w związku z przejawianą przez nie zdolnością powrotu do gniazda znajdującego się z reguły w piaszczystej glebie porośniętej rzadką roślinnością trawiastą.

Analizę budowy wewnętrznej oczu przeprowadzono na podstawie rysunków przekrojów: czołowego, strzałkowego i poziomego, sporządzonych z serii fotografii tych przekrojów dokonywanych na materiale konserwowanym w etanolu.

Stwierdzono niejednorodną budowę oka. Najmniejsze kąty tworzą ommatidia skierowane do przodu oraz położone w pobliżu „równika” oka. We wspomnianych częściach przekrojów kąty w płaszczyźnie strzałkowej są mniejsze od kątów w płaszczyźnie poziomej — ich stosunek dla sektorów o minimalnych kątach wynosi ca 1 : 2.

Pole wzrokowe oka samicy *Bembex rostrata* (L.) w płaszczyźnie czołowej obejmuje $\times 207^\circ$, w płaszczyźnie strzałkowej $\times 235^\circ$ i w płaszczyźnie poziomej $\times 165^\circ$.

Pole dwuocznego widzenia w płaszczyźnie czołowej ku górze obejmuje $\times 50^\circ$, ku dołowi $\times 40^\circ$, do przodu zaś w płaszczyźnie poziomej $\times 60^\circ$.

Z odpowiednich obliczeń wynika, że ocena odległości ku dołowi w związku z tym jest możliwa w granicach 3-66 mm, poziomo ku przodowi w granicach 1,5-80 mm. Zdolność rozdzielcza (minimum separabile) ku dołowi w płaszczyźnie czołowej wynosi teoretycznie $2^\circ 54'$, a w płaszczyźnie strzałkowej 4° ; ku przodowi w płaszczyźnie poziomej: $4^\circ 08'$, a w płaszczyźnie strzałkowej $1^\circ 28'$.

Przy krytycznej częstotliwości zlewania migotania ocenionej na podstawie wstępnych eksperymentów na ok. 165/sek, owad ma teoretycznie zagwarantowaną możliwość dostatecznego rozróżniania szczegółów podłoża, lecąc z prędkością 1,7 m/sek na wysokości 15 cm albo z prędkością 4,5 m/sek na wysokości 39 cm. Są to wartości bardzo bliskie obserwowanych w naturze.

ЗАМЕЧАНИЯ КАСАЮЩИЕСЯ ЗРЕНИЯ У *BEMBEX ROSTRATA* L. (HYMENOPTERA, SPHEGIDAE)

РЕЗЮМЕ

Заданием этой работы была вступительная оценка оптических свойств сложных глаз самок *Bembex rostrata* L. в связи с обладанием ими свойства поворота в гнездо находившиеся как правило в песчаной почве поросшей изредка травянистой растительностью.

Анализ внутреннего строения глаз произведено на основании рисунков фронтальных, медиальных и горизонтальных разрезов, сделанных из серии фотоснимков материала фиксированного в этиловом спирте.

Констатировано неоднородное строение глаза. Самые малые углы создают омматидия направленные вперёд и лежащие в близости экватора глаза. В упомянутых пределах разрезов углы медиальной поверхности являются меньшими чем углы поверхности горизонтальной- их соотношение для секторов о минимальных углах имеется как 1 : 2.

Поле зрения самки *Bembex rostrata* L. во фронтальной поверхности имеет $\times 207^\circ$, в поверхности медиальной $\times 235^\circ$ и горизонтальной $\times 165^\circ$. Поле двойного зрения во фронтальной поверхности вверх имеет $\times 50^\circ$, вниз $\times 40^\circ$ а вперёд в горизонтальной поверхности $\times 60^\circ$. Из соответствующих исчислений следует, что оценка расстояния в связи с этим является возможной в пределе 3-66 мм, горизонтально, вперёд в пределе 1,5-80 мм. Разрешаю-

шая способность (*minimum separatum*) вниз в поверхности фронтальной имеется теоретически $2^{\circ}54'$, а в поверхности медиальной 4° , вперёд в поверхности горизонтальной $4^{\circ}08'$ а в поверхности медиальной $1^{\circ}28'$.

При критической частоте мелькания оцененной на основании предварительных экспериментов на около 165/сек., насекомый имеет теоретическую возможность достаточного различения подробностей среды лета со скоростью 1,7 м/сек. на высоте 15 см или со скоростью 4,5/сек. на высоте 39 см. Такими являются стоимости очень близкие наблюдаемым в природе.

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