

Larval characters and their ontogenetic development in Fulgoroidea (Homoptera, Cicadina)

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Special larval characters and characters undergoing age-dependent development are considered: sensory pits, placs, spinulation on tibiae and tarsi, and wax-pore plates. For sensory pits, the pattern of arrangement and orientation in relation to the body axis, order of multiplication from instar to instar, and evolutionary trends are considered in various taxonomic groups, which were already investigated (Dictyopharidae, Delphacidae). A hypothetical groundplan of sensory pits arrangement is proposed and its deviation in various tagma and segments is presented. Hypotheses of the arrangement of placs and the sequence of their age to age multiplication are discussed. Characteristics of the arrangement and development of spines on tibiae and tarsi are given. A hypothesis of reversible fusion of thick seta with its high socle is proposed. Macroevolutionary system of transformations of spine groups on tibiae and tarsi, which is open to diverse reorganization, including reversions (morphocycle), is reviewed and demonstrated. Some characteristics of the arrangement of abdominal wax-pore plates and trends in their evolution are discovered. The importance of investigation of larval development in Fulgoroidea for taxonomic and phylogenetic purposes is stated.

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Study of larvae in the Fulgoroidea has advanced considerably in the last twenty years, especially with respect to last instar larvae, but also with respect to the whole larval phase of ontogeny. The fifth (last) instar larvae are the most available for collecting and nearly always the most convenient for diagnostics of species and genera. But comparative studies into the whole larval ontogenesis have become especially important for the purposes of the suprageneric classification and phylogeny, and for understanding of evolution of suprageneric groups.

At present, a more thorough and detailed approach to description and evaluation of used characters is required, these characters having already proved highly relevant for the phylogenetic analysis of some groups, e. g. Dictyopharidae and Delphacidae (Emeljanov, 1994a, 1994b, 1995). For instance, it does not suffice to indicate only the number of sensory pits on some body parts, the number of placs on the second antennal segment, or the number of teeth at the apex of hind tibia. Their arrangement, homology and succession of their appearance in ontogenesis should be taken into

consideration. A more detailed approach sometimes shows tentatively established affinities, assessments of polarity of characters or of their taxonomic weight to be erroneous.

Age changes affect body proportions, particularly those of the head and wing-pads, the number and disposition of sensory pits, shape and proportions of antennae; number of ommatidia in eyes, many details of leg structure (first of all, of hind legs), appearance and development of external genital rudiments, and shape and disposition of wax pore plates (if present).

Sometimes the number of larval instars may also change. The primary and standard number of larval instars is five, sometimes it is decreased to four; a case of secondary five-instar development is known (Figs 1-5). The larval development is generally subdivided into prenympal stage (first to third instars) and nymphal stage (fourth and fifth instars), in the latter the wing pads are increasing. Within the prenympal stage, the first instar characterized by the absence of antennal sensillae and the rounded-compact "baby-like" habitus may be separated. In Dictyopharidae, I distinguish a phase A – the first instar, phase B – the second

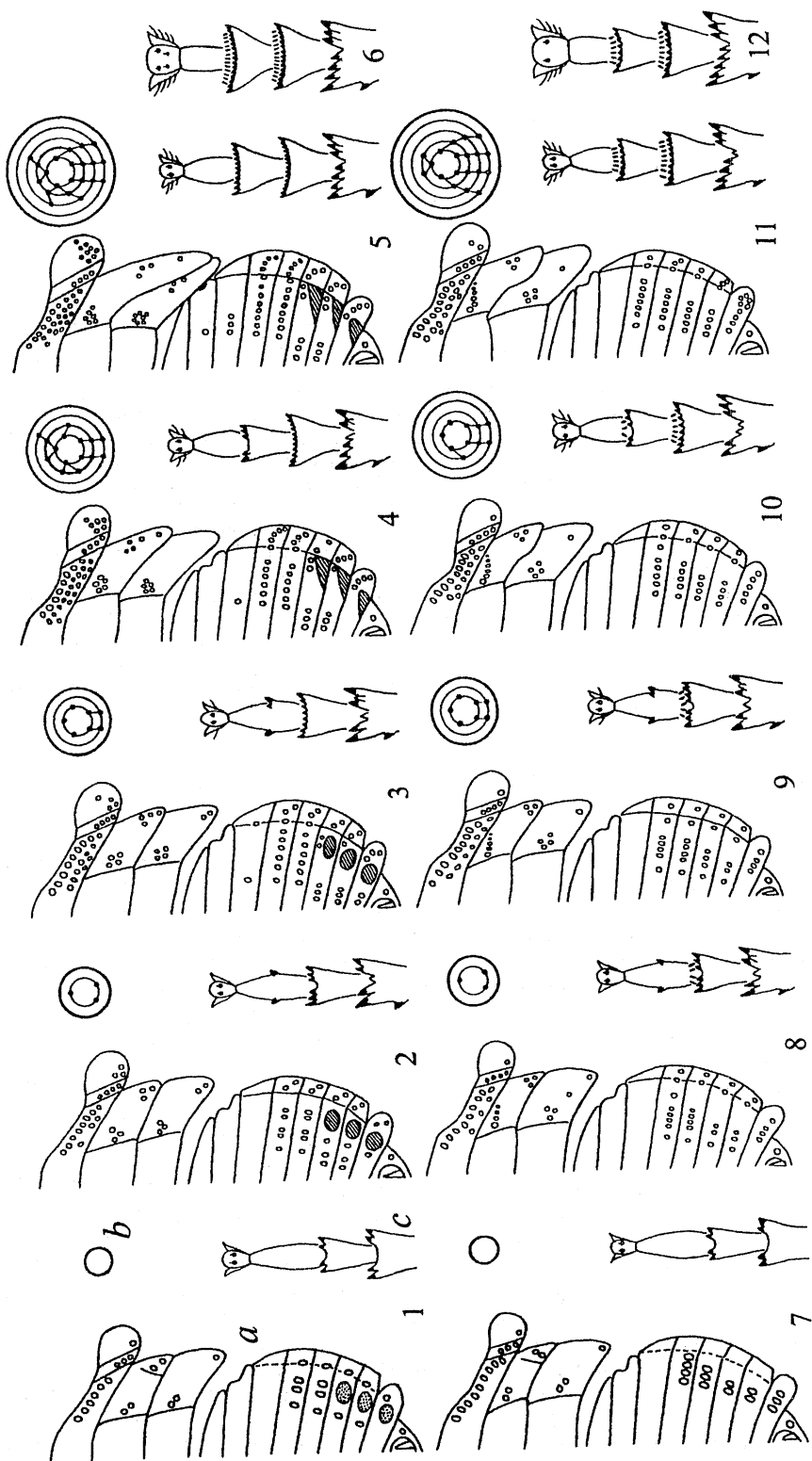


Fig. 1. Schematic representation of several body parts of dictyopharids in larval instars and imagines (after Emeljanov, 1980, with additions). 1-6, *Dictyophara pammonica* Germ. (1-5, larval instars; 6, imago), 7-12, *Elysiaca ferganensis* Osh. (the same). a, tergal parts of thorax and abdomen; b, scheme (maps) of second antennal segment, distal polar projections (fore side situated on the left), circles ("parallels") and lines ("meridians") show disposition and consequence of appearance of places in ontogenesis; c, distal part of hind leg (apex of tibia, tarsus, praetarsus), ventral view.

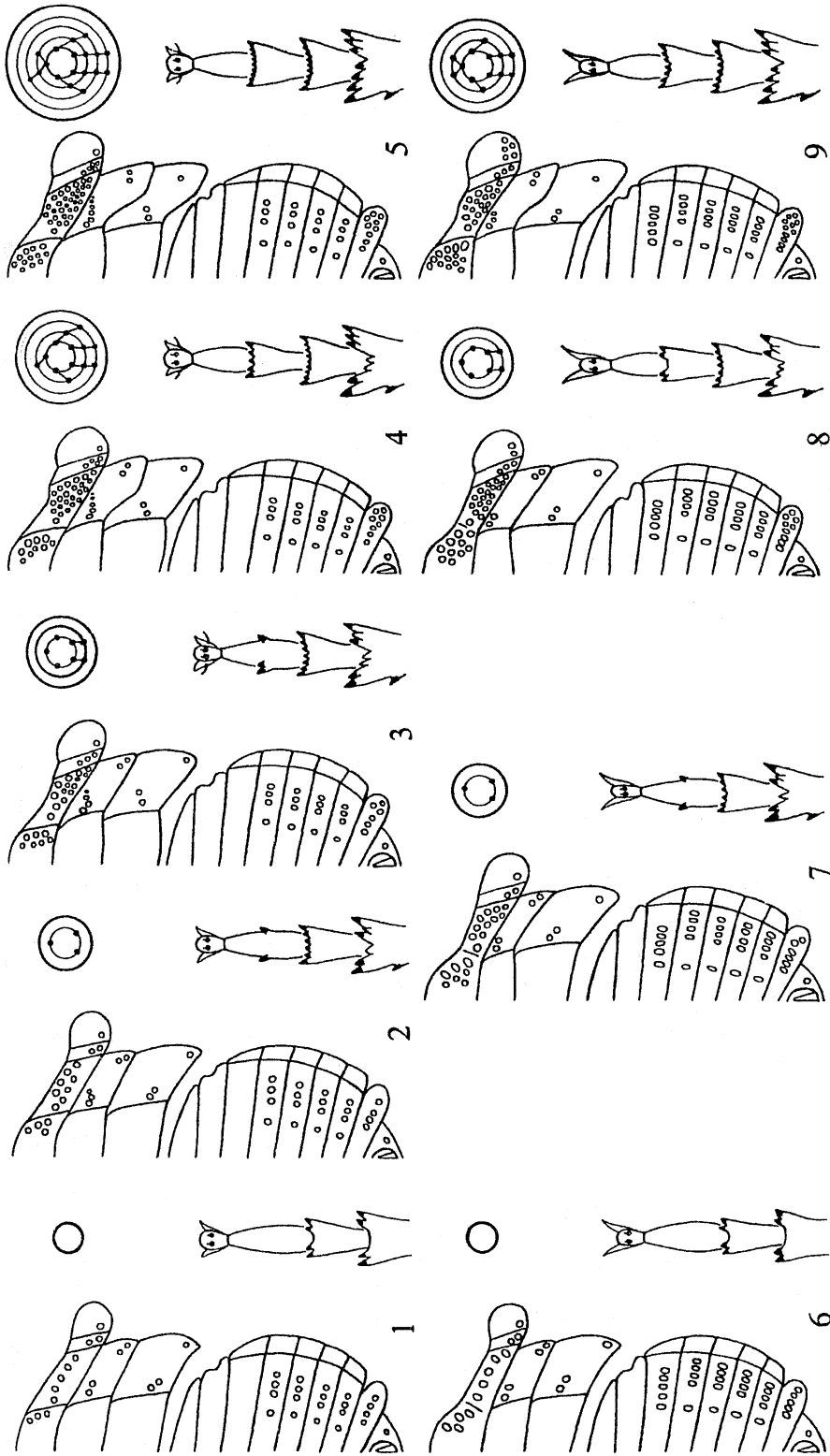


Fig. 2. Schematic representation of several body parts of dictyopharid larvae in various instars (after Emeljanov, 1980, with additions). 1-5, *Nymphorgherius ivanovi* Kusn.; 6-9, *Orotetix jazarzensis* Osh. Designations as in Fig. 1.

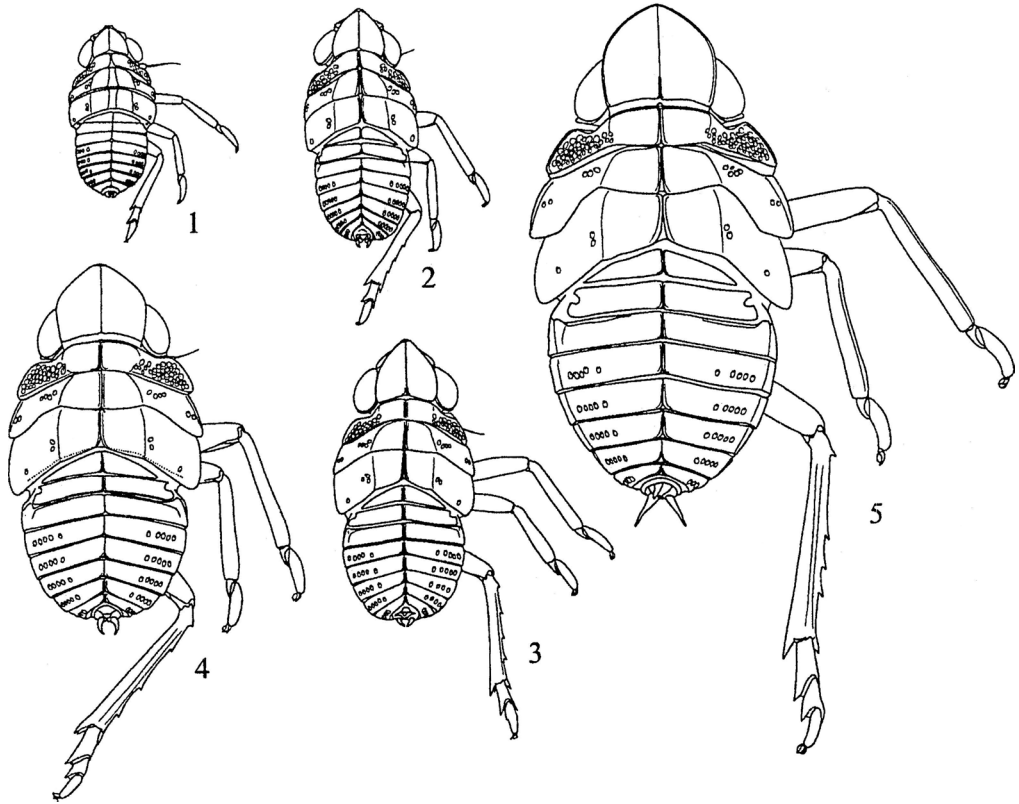


Fig. 3. *Haumavarga fedtschenkoi* Osh., dorsal view of 1st-5th instar larvae (after Emeljanov, 1994b).

and third instars, and phase C – the fourth and fifth instars (nymphs).

The progressive phylogenetical reorganization of ontogenesis in short and observable periods of evolution is normally related to the differentiation of serial characters and frequently to their diminished or completely arrested individual development.

Sensory pits

Sensory pits are specific organs of fulgoroid larvae present in all families except Tettigometridae and Hypochthonellidae (Yang & Yeh, 1994). The latter case of absence is undoubtedly secondary, but the former one is unclear because the phylogenetical position of Tettigometridae is not yet determined with confidence.

The sensory pit is a small hole with a horizontal seta directed inwards and diverging from its border; the length of the seta is not greater than diameter of the hole (Šulc, 1928,

1929; Liebenberg, 1956). Precursors or sister constructions (Fig. 6) may be observed in Membracidae and Aphrophoridae (Cercopidae s. lato?).

Sensory pits are of strictly tergal nature (the only known exception is *Alleloplasis* with sensory pits on the seventh abdominal sternite); they are present on metope and preocular area of the head, on thoracic nota and abdominal tergites.

The primary arrangement of pits on the thorax and abdomen probably was uniform, but it became strongly and differently modified on prothorax, pterothorax and abdomen (Fig. 7). There is a strong temptation to compare the groundplan arrangement of sensory pits with that of abdominal setae in cicadellid larvae, but I have not done that.

The number of sensory pits in the first instar larva is the minimum, and their disposition on thorax and abdomen is more similar. In younger instars, thoracic and abdominal tergites generally are more similar to each other.

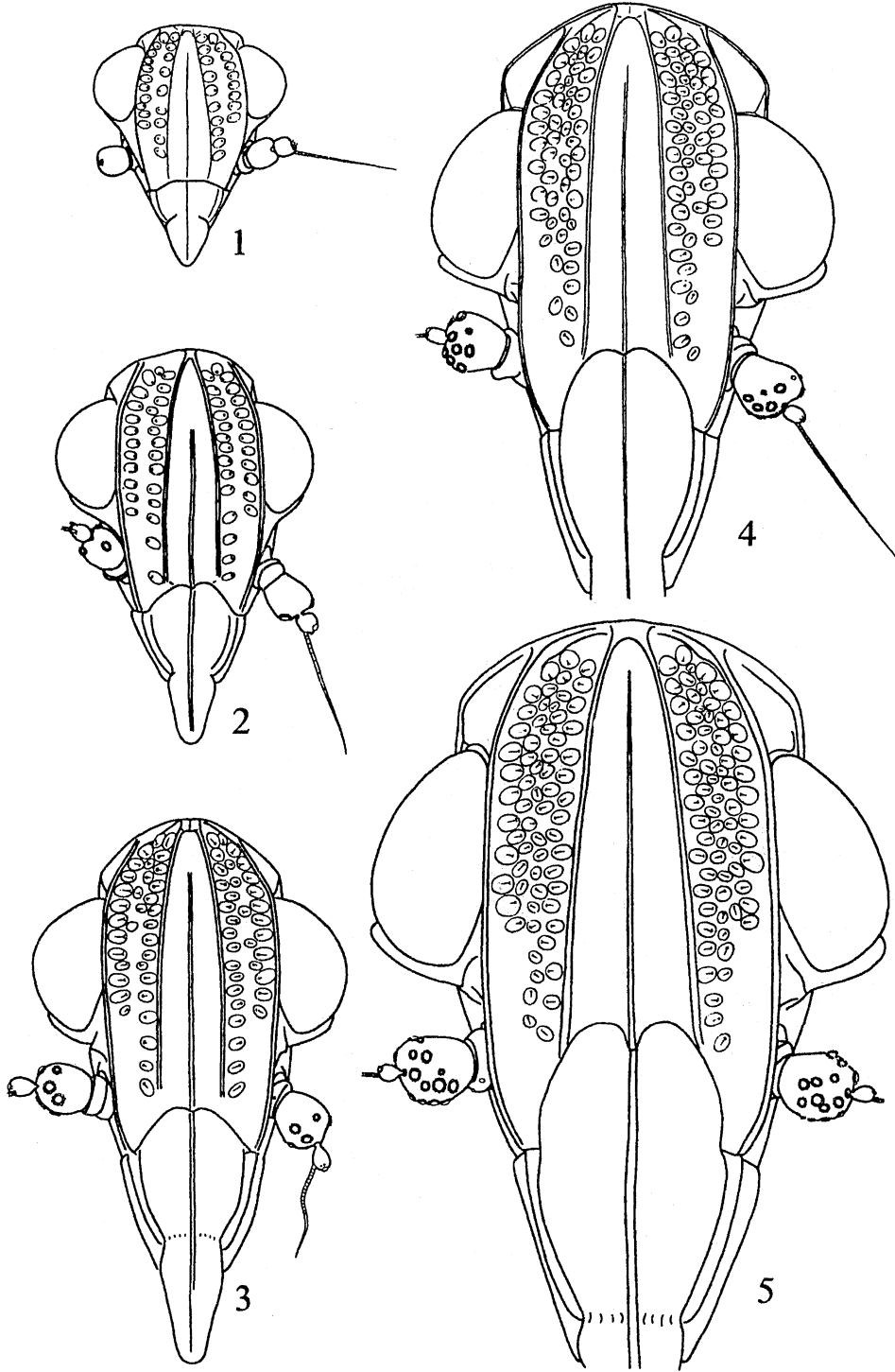


Fig. 4. *Haumavarga fedtschenkoi* Osh., face of 1st-5th instar larvae (after Emeljanov, 1994a).

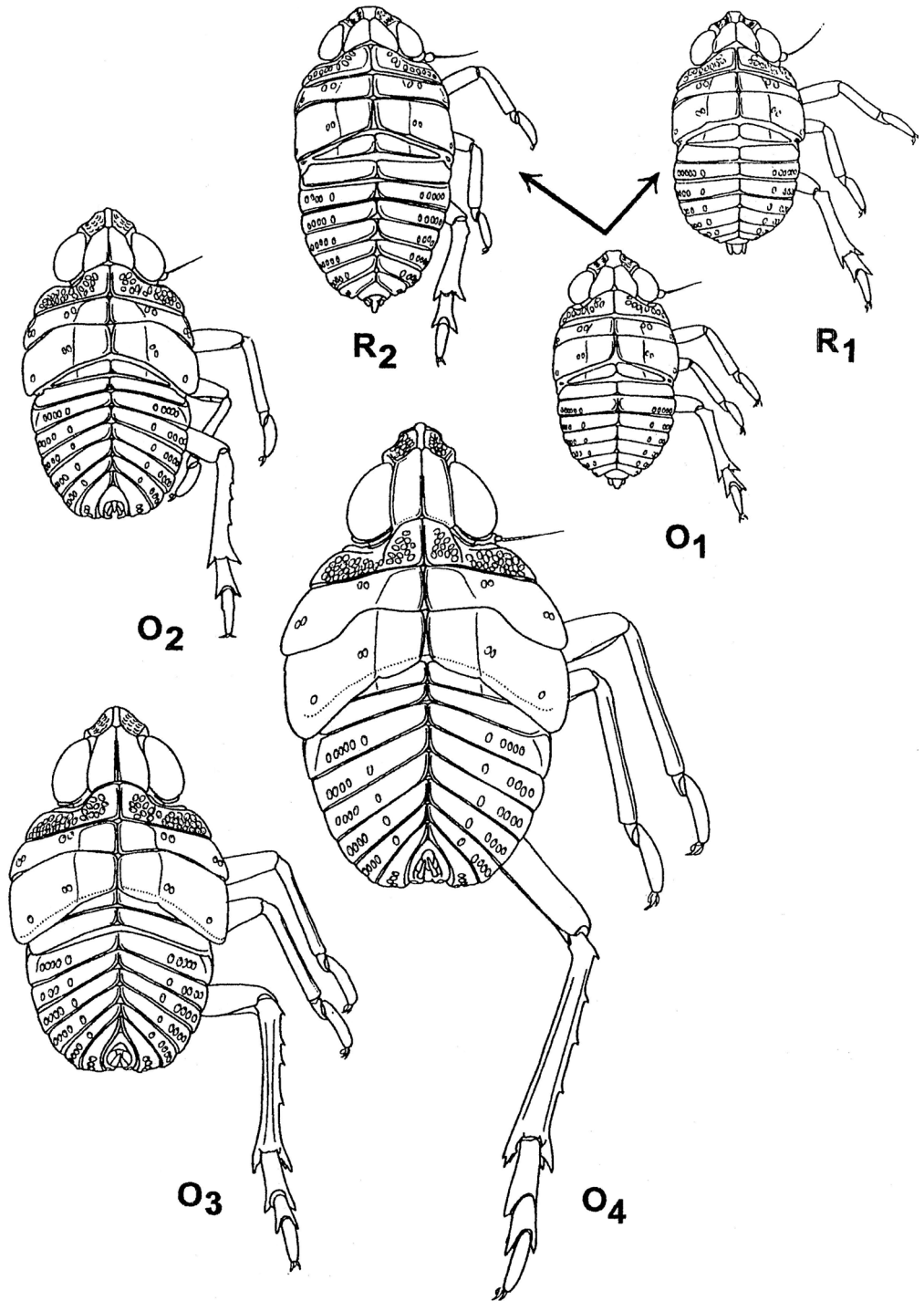


Fig. 5. Larvae of *Ototettix jaxartensis* Osh. and *Repetekia orbicularis* Osh. (after Emeljanov, 1994b, combined). O1-O4, larvae of *O. jaxartensis*, 1st-4th instars accordingly, R₁, and R₂, larvae of *R. orbicularis*, 1st and 2nd instars accordingly, these two instars correspond to the first instar of *O. jaxartensis*.

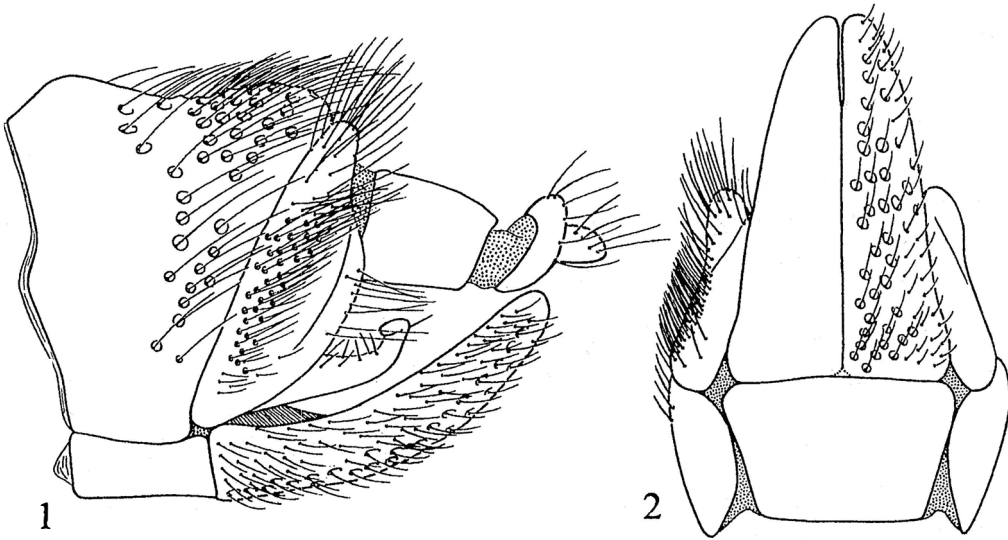


Fig. 6. Genital block of male of *Machaerotypus sibiricus* Leth. (Membracidae) showing analogies (?homologies) of sensory pits (after Anufriev & Emeljanov, 1988).

The disposition and orientation of sensory pits adheres to certain principles. Setae of pits are directed to the margin of tergite or to the keel along which they are situated. The caudal and lateral directions of setae are more typical, but there are some significant exceptions, which will be discussed later.

There are two rows of pits on each side of metope on the head. Generally, the pit setae are directed to the adjoining keel. In Delphacidae, complementary pits are present also on the preocular area, and these pits are likewise directed to the adjoining keel (lateral keel of metope) (Fig. 8). In this situation, a row of sensory pits lies on each side of the keel and the pit setae of the two rows are directed to the keel and hence to each other.

The minimum number of sensory pits on pronotum in the first instar larvae of Delphacidae is six; they are situated in one row, and four groups are recognized by intervals between pits (2+2+1+1) (Fig. 8). Surprisingly, the four medial pits face forward, but two lateral ones, in contrast, backward (as figured by Wu & Yang, 1985). The medial pits are discal-paradiscal, the lateral ones paranotal. The same disposition and orientation of pits (though in different number) was found in Dictyopharidae (Emeljanov, 1994a, 1994b) (Fig. 9), but in Cixiidae and Achilidae the pit orientation is different: all pits face laterally (Yang & Yeh, 1994) (Fig. 10). Origin and ontogeny of these pits allows understanding of these differences.

In my opinion, the mesonotal (and metanotal) disc is homologous not to the disc of pronotum but to the disc + paradisc, consequently the lateral keel of mesonotum is identical to anterodiscal – postocular – lateral sequence of keels in my terminology and to lateral keels in terminology of Yang & Yeh (1994). A short name should be given to this keel; it is present in many representatives of different families (for example, Fulgoridae, Flatidae, Nogodinidae, Ricaniidae, Derbidae) and is represented in larvae by an integrated whole keel.

I think that my terminology is better for imagines, but the terminology of Yang & Yeh is better for nymphs. The lateral keels of pronotum are represented by an integrated keel in nymphs of many families (Fulgoridae, Flatidae, Nogodinidae, Ricaniidae, Derbidae, etc.).

Rendering priority of terminology worked out for imagines, I propose the name “jugal” for this lateral keel. This keel (discal) on mesonotum in primitive forms with numerous pits (*Ugyops*, for example) bears pits on each side in the same way as the lateral keels of metope in Delphacidae. Discal-paradiscal row of pits is bordering this jugal keel medially and consequently its pits face anterolaterally, but the fore part of paranotal row is bordering this keel laterally and its pits face posteromedially, the hind part of paranotal row lies along hind and lateral margins of pronotum and its pits face caudad and, following to the bent of the margin, laterad. Fore (anteromedial) end of

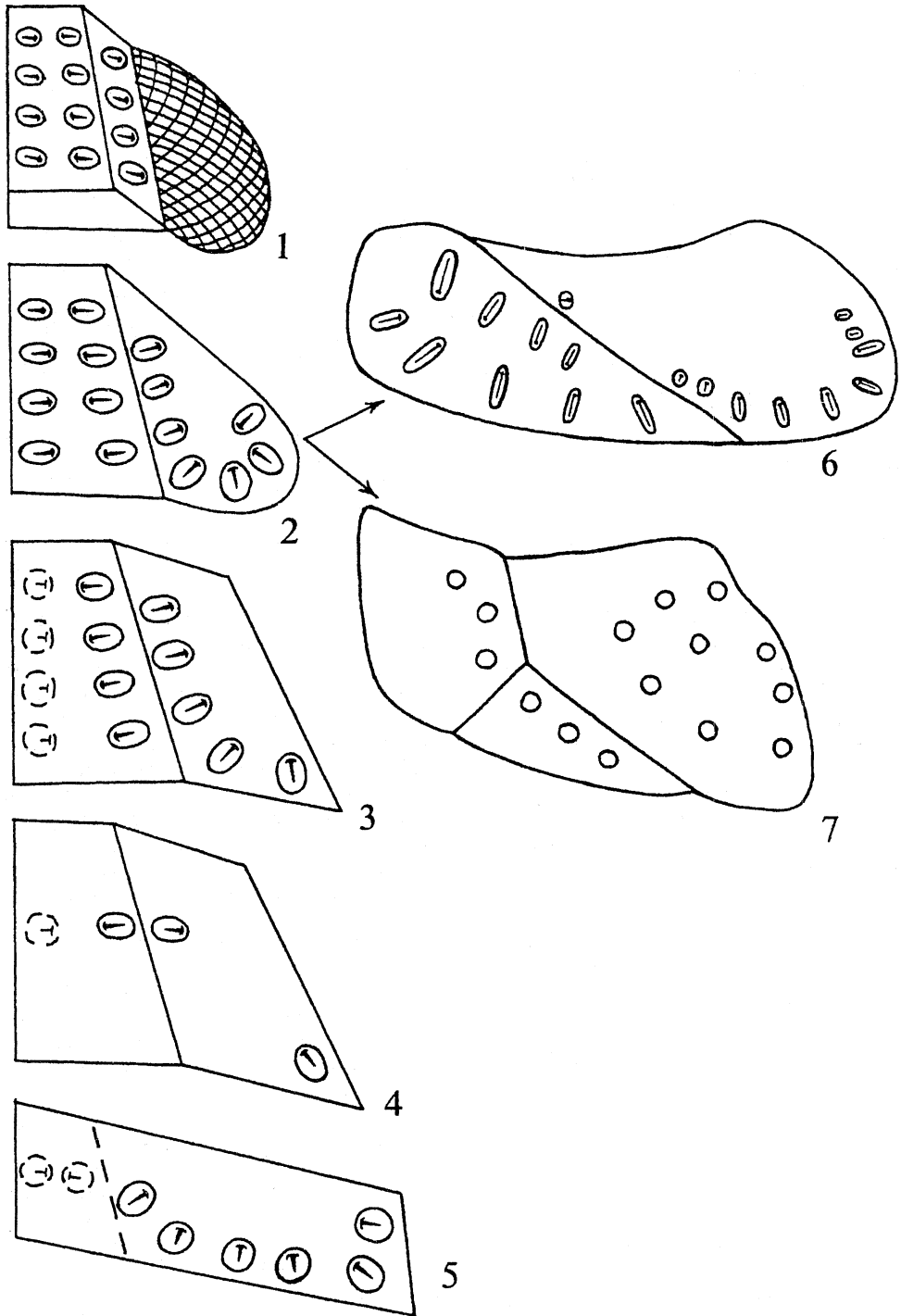


Fig. 7. Hypothetical groundplan of sensory pits disposition in Fulgoroidea (head, pro-, meso-, metanotum and abdominal tergite), compared with real disposition on pronotum in the meenoplid *Nisia carolinensis* Fenn. and derbid *Robigus flexuosus* Mats.

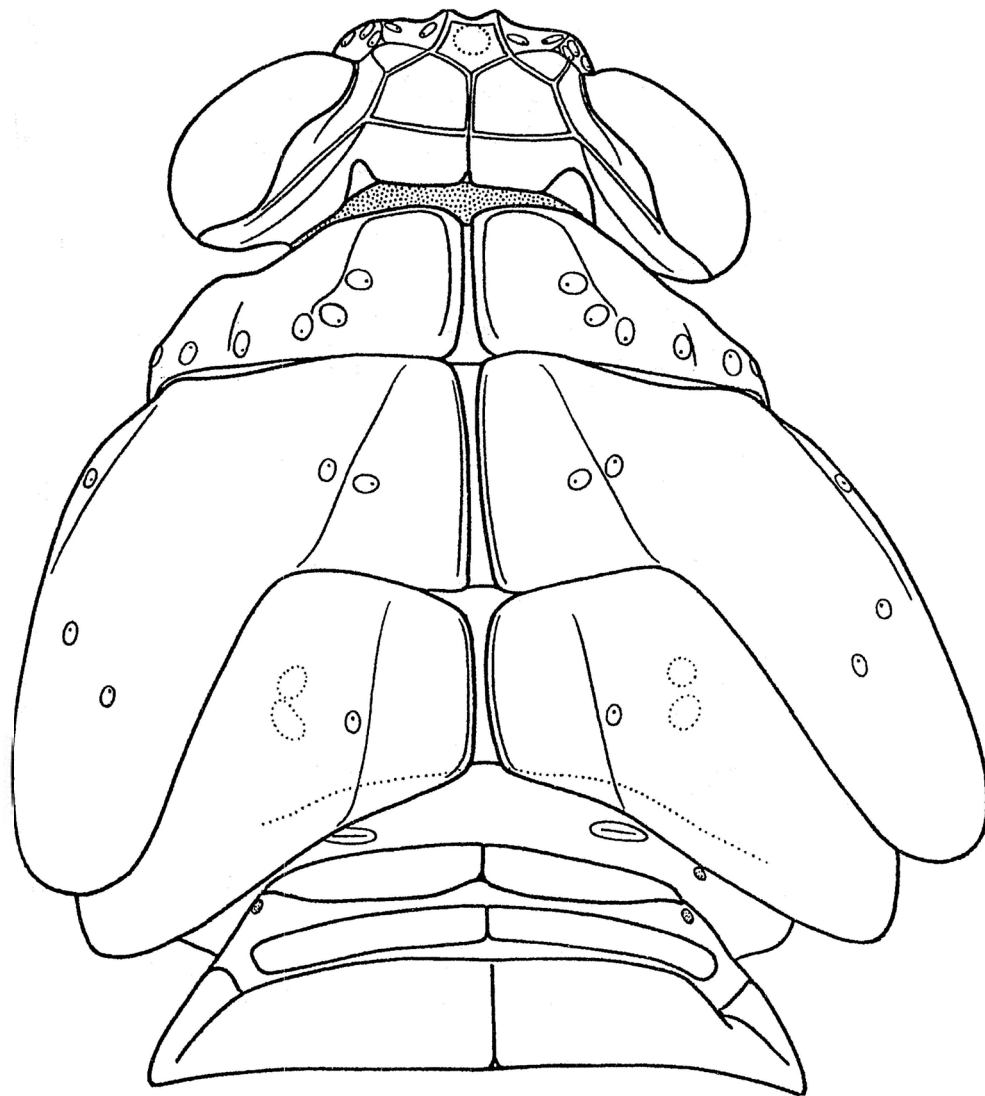


Fig. 8. Fifth instar larva of *Delphax crassicornis* Panz., anterior part of body and basal part of abdomen, dorsal view, showing disposition and orientation of sensory pits.

paranotal row is shifted backward in relation to the discal-paradiscal row; probably, the very first pits are reduced, but this is unclear.

The transverse direction of pit setae in Cixiidae and Achilidae figured by Yang & Yeh (1994) also may be explained. The clue to the explanation is given by orientation of secondary discal-paradiscal pits in Dictyopharidae (*Dictyophara pannonica*, etc.). In the secondary pits, the direction of setae turns to lateral. Consequently, in Cixiidae and Achilidae primary pits have acquired the orientation of secondary pits (due to earlier command for turning).

The comparison of paranotal pits of pronotum with pits of wing pads of meso- and metanotum is difficult because of great reorganization of the wing area.

Though the secondary orientation of pits which face laterad is clear, the initial position from which the pits are turned remains obscure. As larvae of Meenoplidae and Dictyopharidae (*Scirtophaca* and others) evidence, the pits of the second row (primary) face backward (Figs 9: 2; 10: 6). Usually the secondary generation of pits is oriented as initial one (in *D. pannonica* – forward), or is a little deviated.

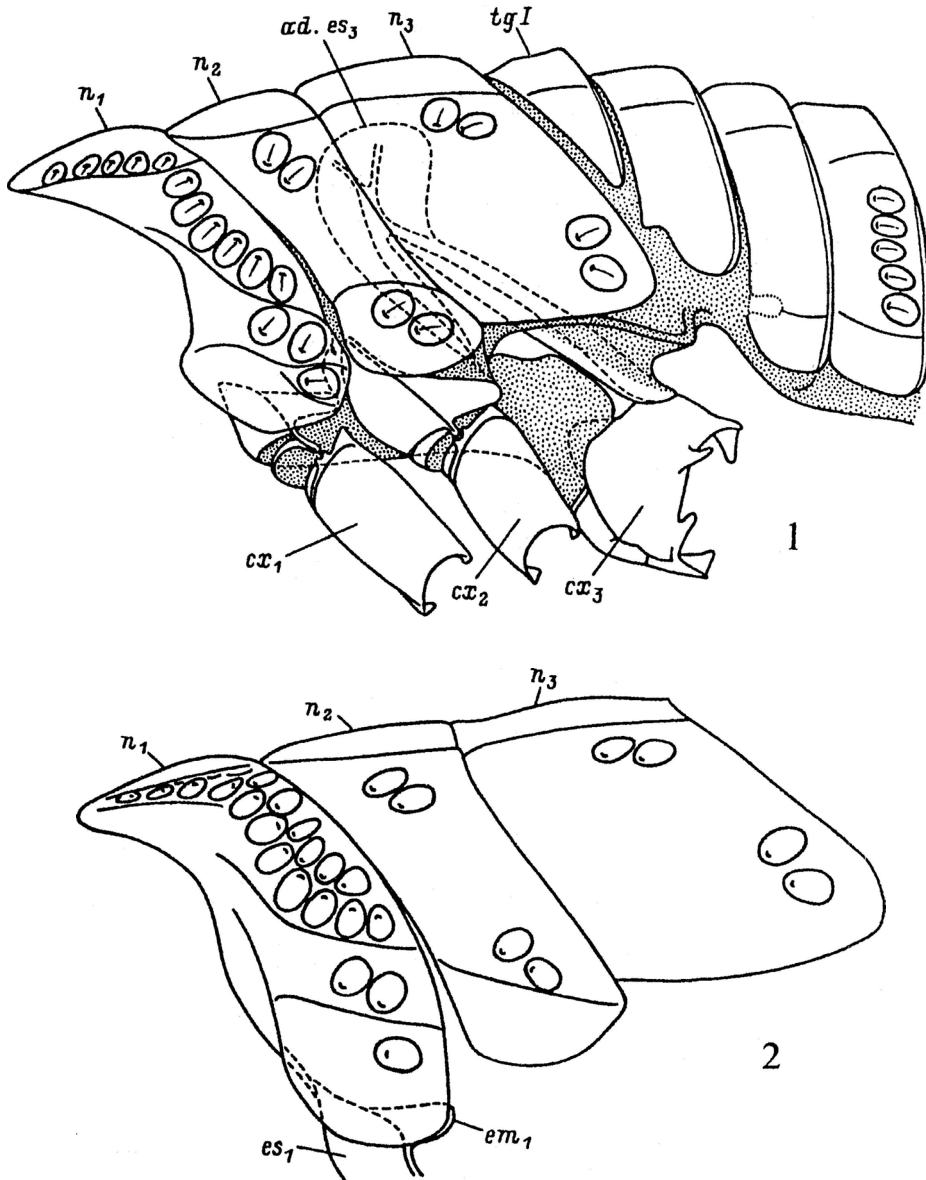


Fig. 9. First and second instar larvae of *Scirtophaca junatovi* Em., left lateral side view, showing disposition and orientation of sensory pits (after Emeljanov, 1994a). 1, first instar, thorax; 2, second instar, thorax and basal part of abdomen. *ad. es*, episternal apodeme of metathorax; *cx*, coxa; *em*, epimeron; *es*, episternum; *n*, notum; *tg I*, first abdominal tergite.

To judge from *D. pannonica*, the fore discal-paradiscal row has subordinated the primary hind discal-paradiscal row, i. e. hind discal-paradiscal row became secondary.

Ontogenetically, pits may be divided into primary and secondary ones, or better to say main and subordinate or derivative. Usually the primary pits are larger than the secondary ones and have more constant size and position. Mul-

tiplication of main pits (Fig. 11) leads to increasing of their number in the already existing row, but appearing and multiplication of secondary pits occurs unilaterally across the primary pit row, secondary pits frequently diminish gradually. A row of main pits also may be desorganized or partly doubled, due to transverse duplication of an individual pit, or by lateral displacement into half step of a new pri-

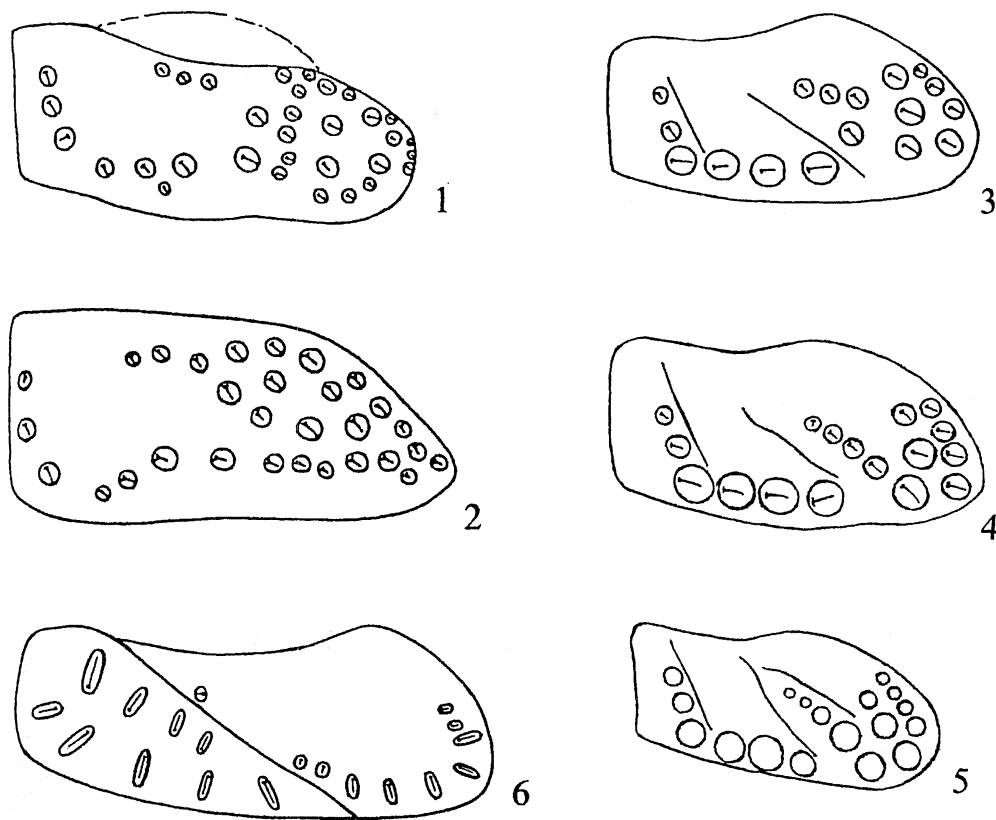


Fig. 10. Right half of pronotum of cixiid (1-2), achilid (3-5) and meenoplid (6) larvae, last (fifth) instars (after Yang & Yeh, 1994). 1, Cixiini sp. 4; 2, *Mundopa kotoshonis* Mats.; 3, Achilidae sp. 3; 4, Achilidae sp. 2; 5, Achilidae sp. 5; 6, *Nisia carolinensis* Fenn. (modified).

mary pit from the row of old ones, when there is lack of space (on metope or pronotum). Secondary pits also are often partly doubled across their row and desorganized. In cases when the pits are numerous, the original arrangement is completely indistinguishable (for example on paranota of Cixiidae). In such cases it is particularly important to trace the development throughout from the first to the last instar.

Another interesting characteristic of pits is their capacity to cross the keel by a leap or with intermediate position on interrupted keel (subcostal keel of fore wing pad, sublateral keels of abdominal tergites, posterolateral keels of pronotum, discal keel of meso- and metanotum in first instar in *Elysiaca*). Remarkably, a pit leaps on mesonotum through the subcostal keel between the first and the second instars.

It should be said also separately about phylogenetic – taxonomic difference between pit

construction (Fig. 12). Significant part of my observations and conclusions is based on excellent drawings in the monograph of Yang & Yeh (1994).

The raised border of sensory pits in Derbidae, Meenoplidae, Delphacidae, probably also Cixiidae has a shape of a horseshoe, is incomplete. Of great interest are pits with a double row of small setiform sensillae, which are present in some tribes of Derbidae: 5 pairs in Zoraidini (3 pairs in Lyddina), 3 pairs in Cenchreini, 2-5, often 3 pairs in Otiocerini; in the tribes Cedusini, Rhotanini, Nicertini, these sensillae are absent. In the majority of higher families of Fulgoroidea beginning from Dictyopharidae and Fulgoridae, the raised border of a sensory pit forms a complete ring. The raised ring is divided in Flatidae into many segments. In the subfamily Ommatidiotinae (Caliscelidae), the border of a sensory pit bears one or two small setiform sensillae (Fig. 12).

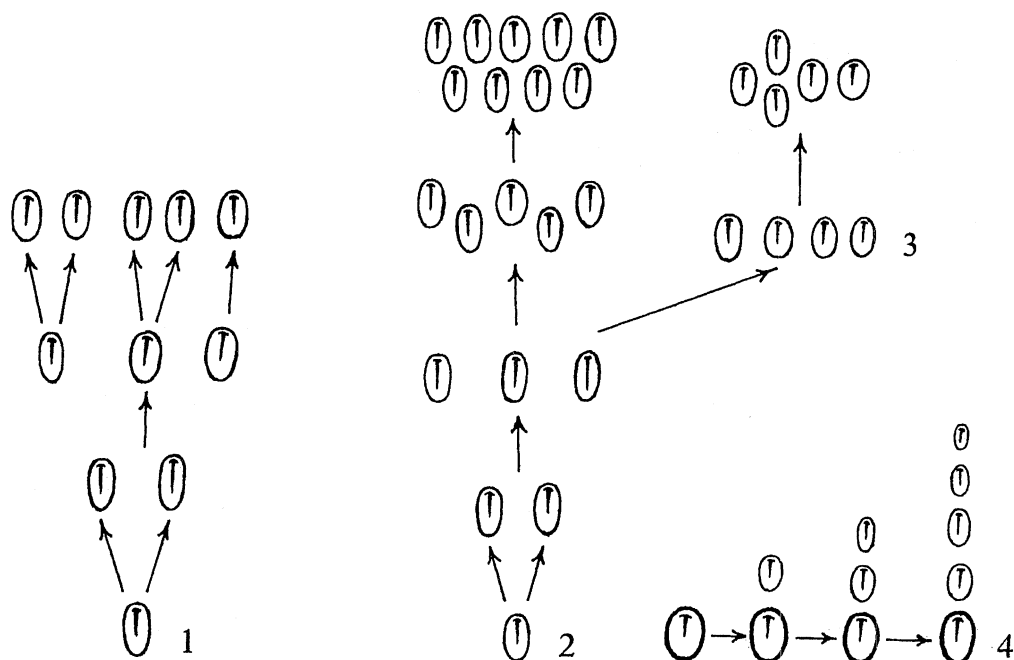


Fig. 11. Ontogenetic multiplication of sensory pits. 1, lateral multiplication; 2, duplication of a row; 3, partial duplication of a row; 4, longitudinal multiplication of a primary sensory pit.

In the tribe Bocrini, the number of these sensillae is varying depending on the instar (Emeljanov, 1999).

Placs on pedicellum of antennae

The increase of number of placs and advent of a pattern in their arrangement throughout instars were described by me (Emeljanov, 1980) in the family Dictyopharidae (Fig. 13) and by Asche (1985) in the family Delphacidae. Simple comparison of these two schemes leads to suggestion of significant differences in disposition and development of placs in these two families. In Dictyopharidae, I distinguish five meridians partly bifurcated; in Delphacidae, Asche distinguishes seven (in one case – eight) simple meridians. However, Asche has given a scheme of plac disposition only for higher Delphacidae, and has shown the ontogenetic development only in *Chloriona*. Analogous data are presented for *Matutinus* (D'Urso & Gulielmino, 1986). For such relatively primitive representative as *Asiraca clavicornis*, Asche gives only the number of placs from in-

star to instar without drawings, but the numbers in *Asiraca* are not identical to those in higher Delphacidae. The recognition of scheme of plac disposition in the majority of cases in Delphacidae, both imago and last instar nymphs, is difficult or impossible because the pedicel is highly modified – styliform or foliately depressed. It is necessary to examine larvae of the second and the third instars in lower Delphacidae. I have not got this material.

I attempted to reveal the plac disposition scheme in an undetermined representative of Eodelphacini directly on a dry, not prepared specimen.

I have found in Eodelphacini the same five meridians as in Dictyopharidae. The very limited material retains naturally a good deal of uncertainty. I suppose that two lower placs in Asche's scheme belong not to the first but to the second parallel (Fig. 14). In any case in Eodelphacini the numbers of placs in lower rows are great and highly diverse as in higher Delphacidae; the same difference may be observed also in the upper row.

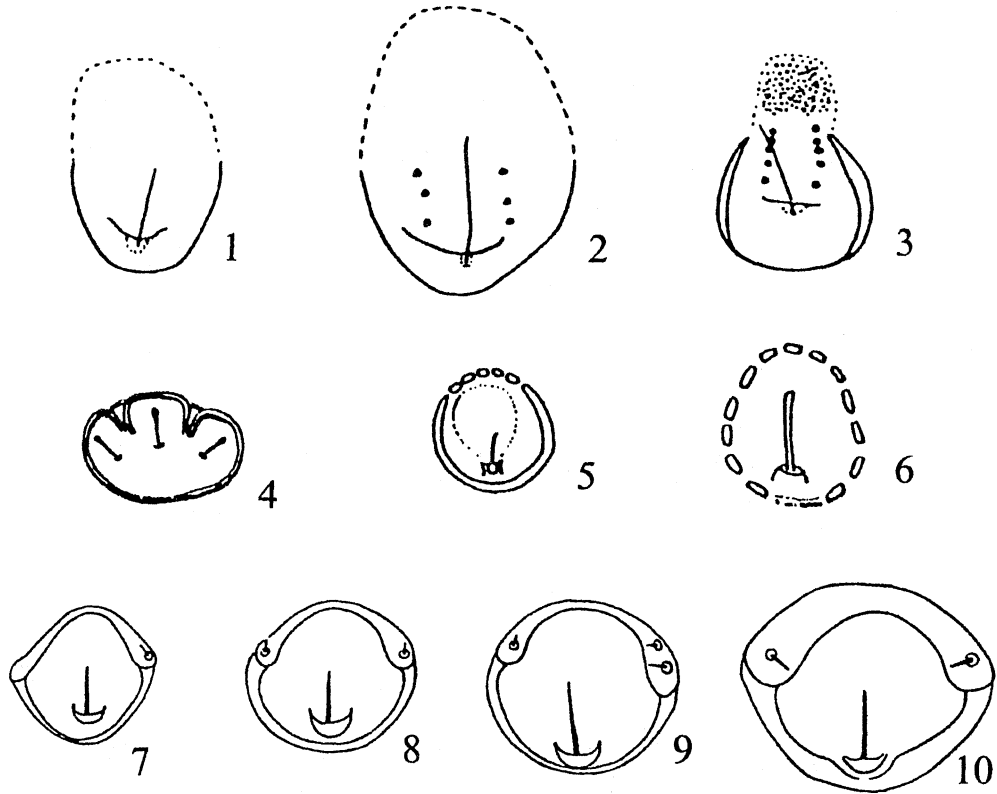


Fig. 12. Sensory pits in larvae of various representatives of Fulgoroidea. 1-6, 5th instar (after Yang & Yeh, 1994): 1, *Rhotana inornata* Yang & Wu; 2, *Nesokaha infuscata* Muir; 3, *Zoraida insolita* Yang & Wu; 4, *Ricanula sublineata* Jacobi; 5, *Flatoides* sp. 3; 6, *Flatoides* sp. 2; 7-10, *Bocra ephedrina* Em. (after Emeljanov, 1999): 7, 1st instar; 8, 2nd instar; 9, 3rd instar; 10, 5th instar.

Eodelphacini is a group (tribe) of great interest as one of the more primitive representatives of Fulgoroidea with larval pits.

The sequence of appearing of placs on antennae is probably of interest in the first line for developing of taxonomic systems predominantly on family and subfamily level, but more important data may be received studying the second-third instar larvae.

If discussing theoretically, which number of meridians is primary, then, considering antenna homologous with leg, the number should be four or six, but it remains now unclear. My observations show that some meridians may duplicate starting from the second parallel, placs in rays (rows) may be also partly doubling across the line. Evidently the wide polymerization, as in Fulgoridae and others, results in multiplication of placs occurring according to more complicated and hardly recognizable programme.

The sequence of appearing of pits of the first ring (of first parallel) is also of interest. In Delphacidae, a pit is added in each instar after the second one, and in the fifth instar all pits of the first ring of my scheme are present. In Dictyopharidae, the first ring is complete already in the third instar, and the fourth instar displays the differences of taxonomic groups within the family.

Spines of hind tibiae and tarsi

Spines are developed in Fulgoroidea nearly always only on hind tibiae and tarsi. It is sufficient reason to suppose that the origin of these spines is due to consolidation (fusion) of a thick, short seta with its large socle. Lateral spines in Cixiidae demonstrate exactly this combination (Fig. 15). Spines on the first and the second tarsomere also may be with or without setae which are usually subapical. Apical

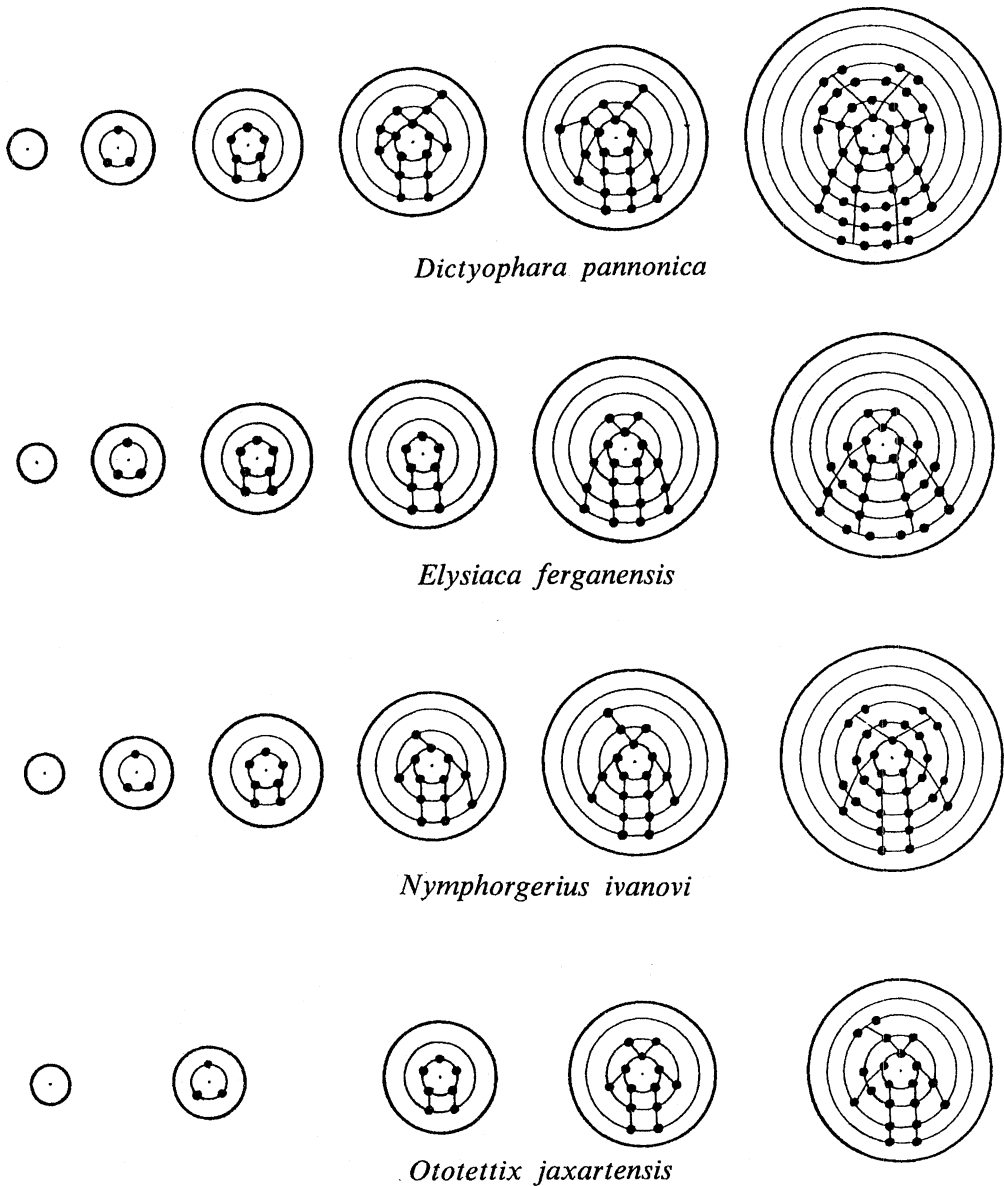


Fig. 13. Ontogenetic development of placid in Dictyopharidae (see also Figs 1-2) (after Emeljanov, 1980). First row, *Dictyophara pannonica*; second row, *Elysiaca ferganensis*; third row, *Nymphorgerius ivanovi*; fourth row, *Ototettix jaxartensis*.

spines of hind tibiae and last lateral spines of tarsi, as far as known, are always simple, without setae. But Hamilton (1990) noted short, thick setae even on apical spines of metatibiae in the extinct Cretaceous family Lalacidae related to Cixiidae (!).

However, as Yang & Yeh (1994) have shown in nymphs of *Basileocephalus germanus* and of

one related undetermined representative of Derbidae, there is a seta at one side of femur and tarsus of hind leg at the place of spine (Fig. 17); an analogous substitution may take place in hind tibia of the fifth instar larvae in *Myndus crudus* (Wilson & Tsai, 1982; Wilson et al., 1984). In the imago, these setae substitute the spines in both cases. It may be supposed, that

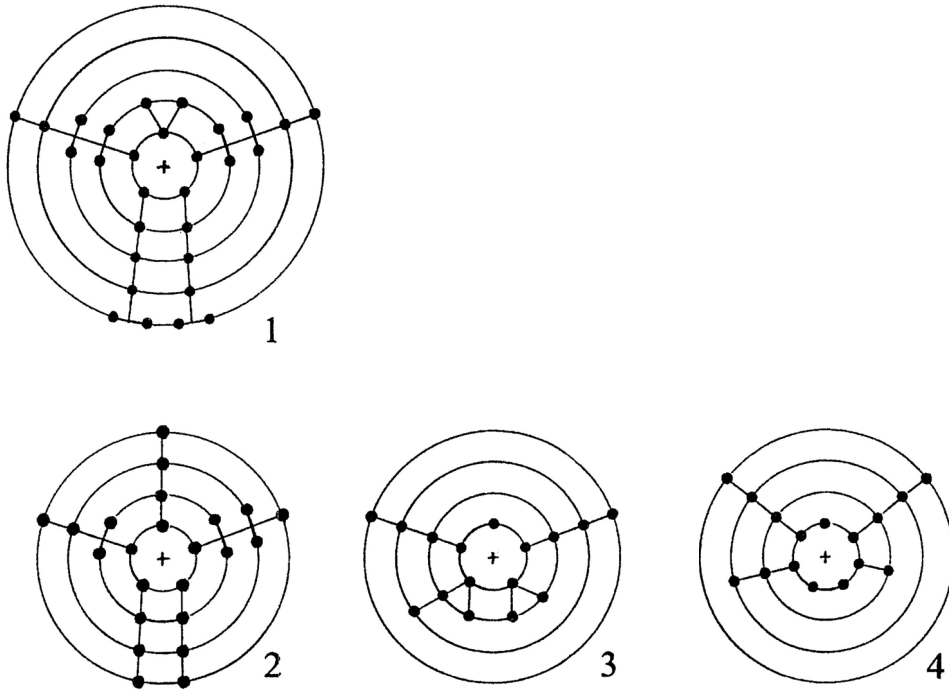


Fig. 14. Arrangement of plac (on second antennal segment) in Delphacidae with reference to Dictyopharidae (see Fig. 1) (after Asche, 1985, Emeljanov, 1980). 1, *Elysiaca* (Dictyopharidae); 2, *Punana* sp.; 3-4, *Chloriona* sp. (3, my interpretation; 4, according to Asche, 1985, slightly modified).

the later phylogenetically the seta with socle develops into spine, the easier it may return to initial state.

Lateral spines of hind tibiae arise commonly in the second instar, in some Delphacidae in the third one. In Dictyopharidae, lateral spines appear in the second instar, except the knee spine, the latter appears in the third instar. Apical spines of hind tibia, as far as our present knowledge goes, are present in the first instar larvae at once, in number of four with a distema (but known data are restricted). However, in the family Tettigometridae (*Euphyonarthex phyllostoma* Schmidt) the spines appear only in the fourth instar (Chen & Yang, 1995).

Interpretation of further increase of spines may be different, since the data are insufficient (Fig. 16). Observations on Dictyopharidae have shown that external and medial spines are increasing unequally (Fig. 18). The third spine of the medial group develops between the first and the second ones, as representative of the second row; the third spine of external group and the following ones develop in the interspace between the two groups. As far as I know, the medial group is not increasing over three spines, there are often only two spines;

the external group may increase nearly unrestrictedly. New spines become of definitive size within one or two instars, that is to say that in one or two instars the spines remain underdeveloped. Although the sequence of spine appearing in the external group shows their uniseriarity, I am not sure of it. Probably we observe a deeply modified secondary situation. In imagines of most of Dictyopharidae, spines of the external group are differentiated in their length and deflection, and form two rows with alternate spines in each row. Regular biseriality of apical tibial spines is probably a common character of all Cicadina, or even Homoptera. The origin of spines from setae offer an easier understanding of the possibility of multiplication of spine rows over the two ones, as realized in Lophopidae.

In the macroevolutionary plane, the programme of development of denticles at the apex of tibia and first and second metatarsal segments has a labile, reversible nature both in relation to the number and arrangement of denticles and in re-articulation or fusion of the (sub)apical spine with its base (Fig. 17). Analogous multivariant series of tibiotarsal denticulation in many Fulgoroidea families are

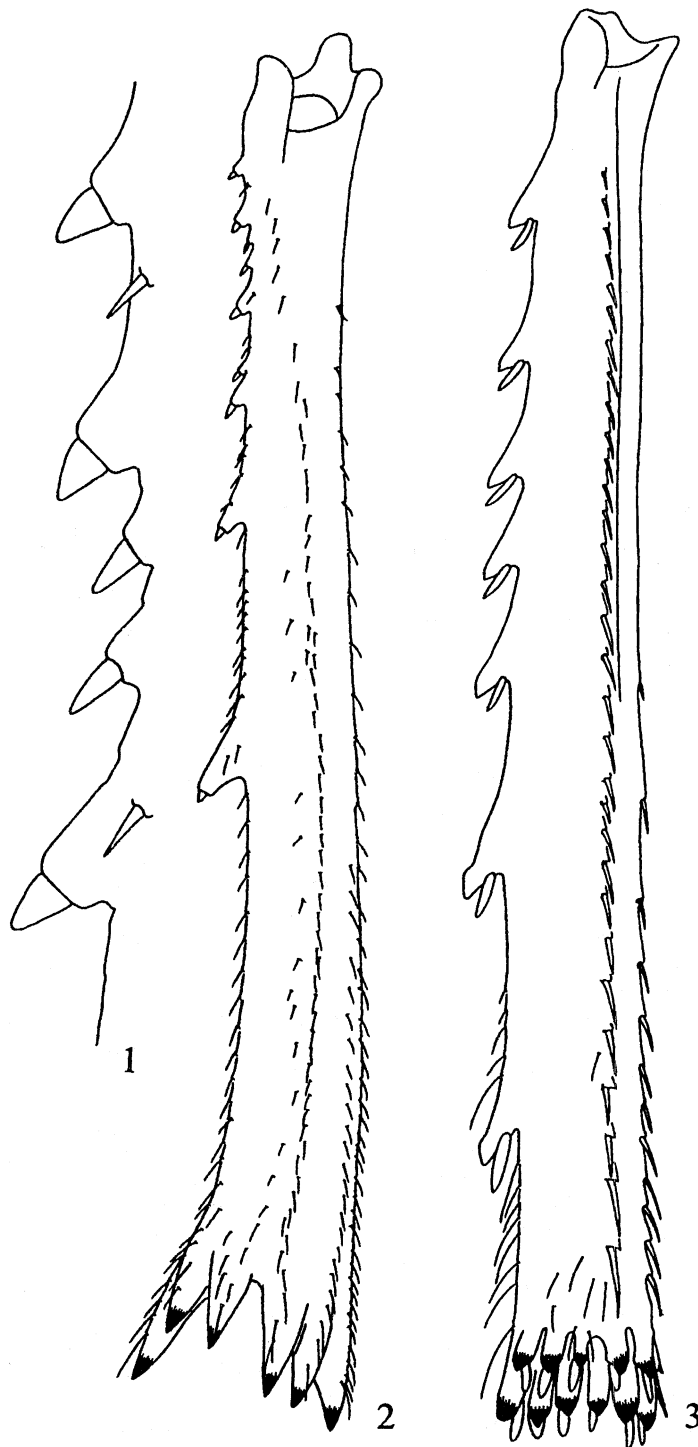


Fig. 15. Hind tibia of Fulgoroidea (1, 2) and Membracoidea (3) (after Anufriev & Emeljanov, 1988). 1-2, *Oecleopsis artemisiae* Mats.; 3, *Ledra aurita* L.

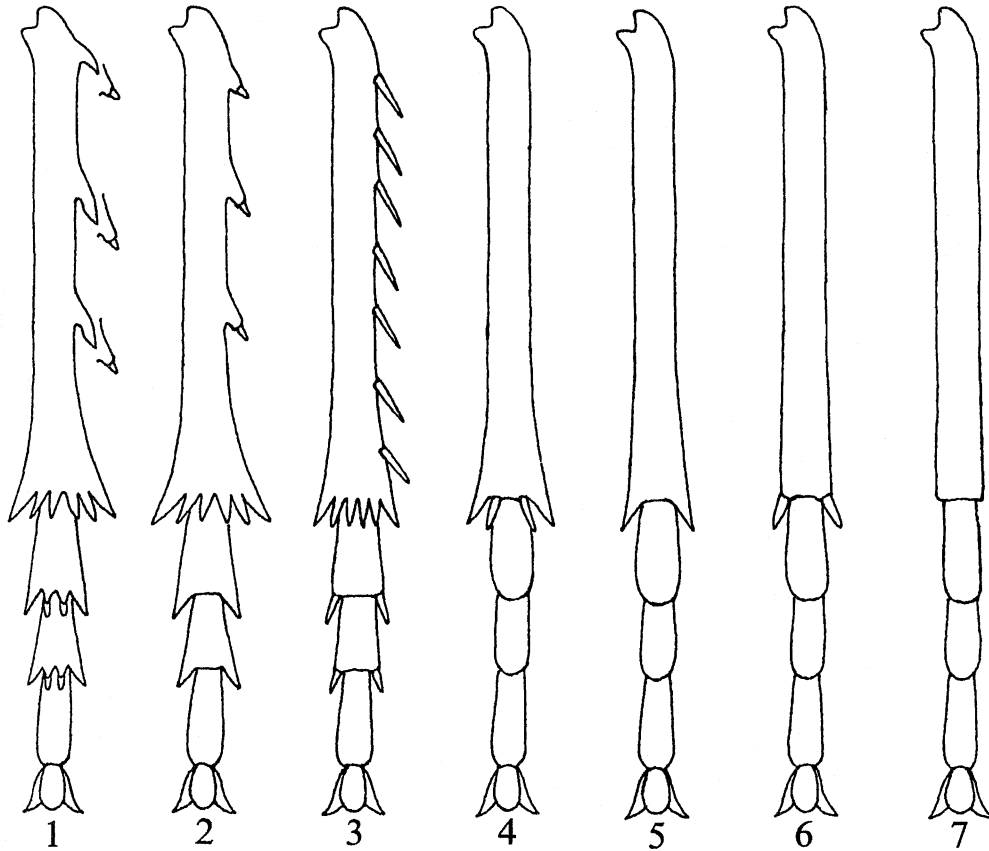


Fig. 16. "Desarmement" of hind leg in evolutionary retrospective.

result of and argument for this mechanism. I have proposed the name *morphocycle* (Emeljanov, 2000) for such repeated series of morphogenetically depending character states.

Development of spines on tarsi (Lindberg, 1939; Emeljanov, 1980; Asche, 1985; Wilson, 1985; Yang & Yang, 1986; Chen & Yang, 1995; McPherson & Wilson, 1995) may be observed from zero. The two lateralmost spines arise first, after that the following spines arise abreast medial to the lateral ones. The two parts join commonly in a state of six spines (3+3). In the majority of cases, all spines are simple, without subapical setae, but in Ranissini (Dictyopharidae) all internal spines, except the lateralmost ones, bear subapical setae (Fig. 18, second row); in other Dictyopharidae, the subapical setae arise in imago only (Fig. 18, first row).

If I may say so, the timing of appearance of the subapical setae in Ranissini is of great interest and comprises two stages. At the first,

the instar is going in which the segment acquires two lateral spines, one on each side (but without subapical setae); these spines arose in the first instar on basitarsus and in the third instar on the second tarsomere. In the next instar, subapical setae appear also; subsequent spines arise at once with setae. Only the first setiferous spine should undergo "a trial period". The subdivision of the distal primordial tarsal segment into the second and the third definitive ones occurs in the next instar after the instar in which the first spines of the future second segment had arisen.

In some Cixiidae and Delphacidae, fore and middle tarsi in the first instar are inarticulate, as figured by Wilson et al. (1984).

The degree of development of pretarsus in last instar larvae, as it is shown in the publication of Yang & Yeh (1994) and Chen & Yang (1995), is very diverse in different representatives, but in the majority of cases the larval development remains unknown. I have

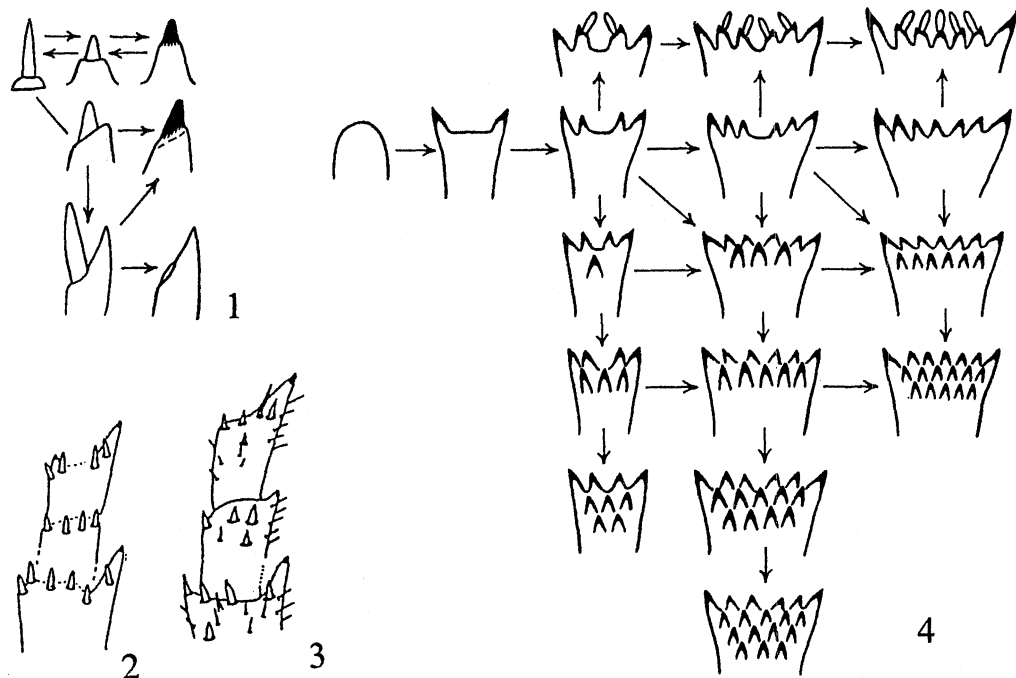


Fig. 17. Reversible evolutionary (morphocyclic) modifications of armature of legs. 1, modifications of seta - tooth; 2-3, tooth and seta on hind legs of Derbidae; 2, "A-ini sp. 1" apex of metatibia and first two tarsal segments, ventral view; 3, *Basileocephalus germanus* Yang & Wu, the same (2 and 3 after Yang & Yeh, 1994); 4, apex of the 1st and 2nd metotarsomeres - morphocyclic evolutionary transformations.

traced the larval development in Dictyopharidae only. In some groups, the number of claw setae increases evenly from one instar to the next one; in other groups, only one seta appearing in the third instar is preserved; in the case of absence of claw setae in imago, these setae are absent in larvae also. In Dictyopharinae, the increasing of the number of sensillae on arolium from two to four takes place only when moulting to imago.

I think that the initial, plesiomorphic state in Fulgoroidea is three claw setae in the fifth instar and four in the imago, this state is present in the slightly advanced Dictyopharidae, which acquire one seta in the third instar. There is normally one pair of chaetoid sensilla on arolium in both nymph and imago; rarely in imago these sensilla are doubled (Dictyopharidae); in *Lophops carinata*, there are two pairs of sensilla already in the nymph (Yang & Yeh, 1994). But in Cixiidae and Achilidae both claw setae and sensilla on arolium are absent in the fifth instar; in *Ugyops*, there is one claw seta and one pair of sensilla on arolium, but the latter sensilla are probably specialized, platella-like (Yang & Yeh, 1994).

Wax-pore plates on abdominal tergites

Wax-pore plates normally are present on the sixth-eighth tergites; they are primarily divided by crosspieces with a sensory pit into six islands (Fig. 19). This state may be seen in Cixiidae. Thus, the primary core of wax-pore islands (probably initial waxpore) is situated behind and between primary sensory pits. In *Myndus* and *Oecleus* (Wilson & Tsai, 1982; Wilson et al., 1984), the larvae of the first instar hatch with two islands divided by one crosspiece, then in each instar one more island is added. In junior instars, the wax-pore plates lie on tergite surrounded by its sclerotization and in its plane, but in senior instars the wax-pore plates turn out to be on the hind border of the tergite bent to vertical position. The moment of inclination in Cixiidae is not refined. In Dictyopharidae (Dictyopharinae), the wax-pore plates quit the tergite plane when moulting into the fourth instar.

In the branch Kinnaridae-Achilidae, the wax-pore plates in immature stages are diminished or reduced to one pore or are completely absent, as in Meenoplidae. The situation in Kin-

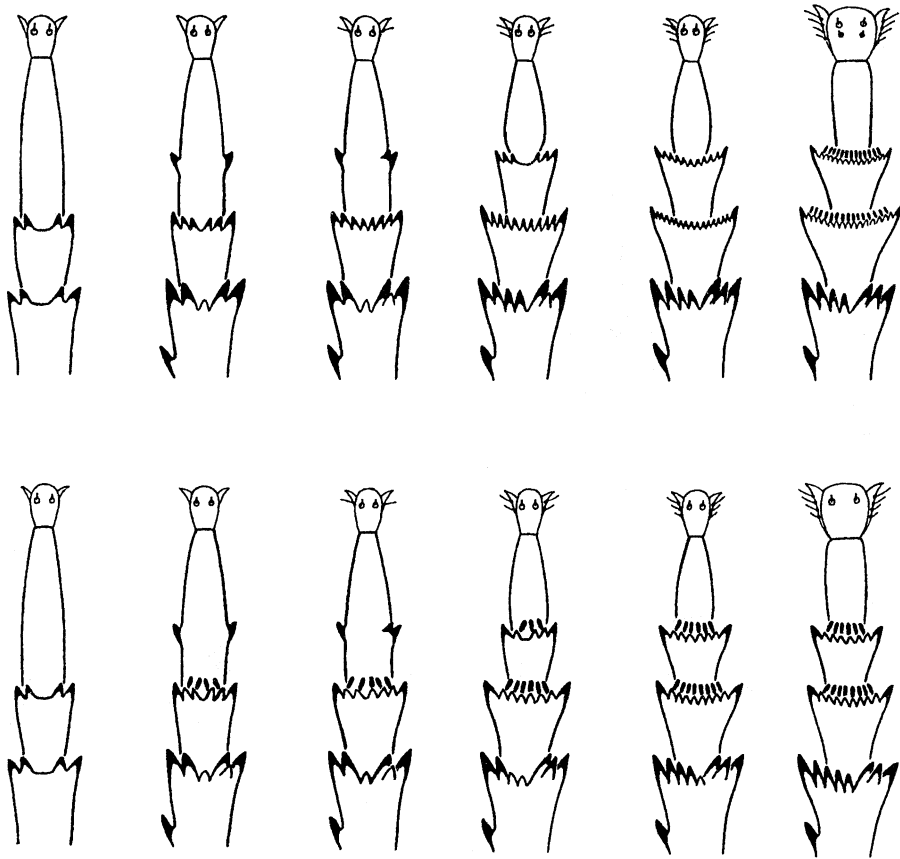


Fig. 18. Ontogenetic development of hind leg apex in Dictyopharidae, diagrammatic (after Emeljanov, 1980, modified). First row, *Dictyophara pannonica*, second row, *Elysiaca ferganensis*.

naridae is unknown. Nymphs of Kinnaridae were seen by Fennah, but not described and probably not preserved. In Achilidae, there is only one wax-pore plate of unknown origin (as to one or more islands have been included in the plate). In Derbidae, as Yang & Yeh (1994) have shown, the wax plate is reduced to one specialized pore. These pores are present in number of one or two on each side of tergite and situated in its medial part. It is very likely that the plate of Achilidae and isolated pores of Derbidae correspond to two initial islands in first instar larva of Cixiidae. Larval development in these two families was not investigated also.

In the branch Dictyopharidae-Fulgoridae, fusion of primary islands or reduction of part of them results in two plates per half tergite in Fulgoridae or one plate per half tergite in Dictyopharidae. In the examined Dictyopharinae, only one plate is present, and ontogenesis does not provide any indications as to its genesis.

The more lateral position of dictyopharid wax-pore plates makes us to think that they have not included the two primary medial islands. Both peculiarities of wax-pore plates composition have occurred already in Fulgoridae-Dictyopharidae: grouping of all plates into one vertical plane and reduction of wax-pore plates on the sixth segment.

In contrast to the lower Fulgoroidea, in the higher Fulgoroidea the number of initial wax-plate islands is decreased to five due to loss of the medial one, as Yang and Fang (manuscript) rightly consider. It may be supposed that the two medial islands, which are present in the first instar larvae of Cixiidae, have early separated functionally and therefore their evolution was going on separately.

Ontogeny of higher Fulgoroidea was described very superficially and with a small number of examples. In Flatidae, the wax-pore plates on the sixth tergite are strongly regressed and their development has been ar-

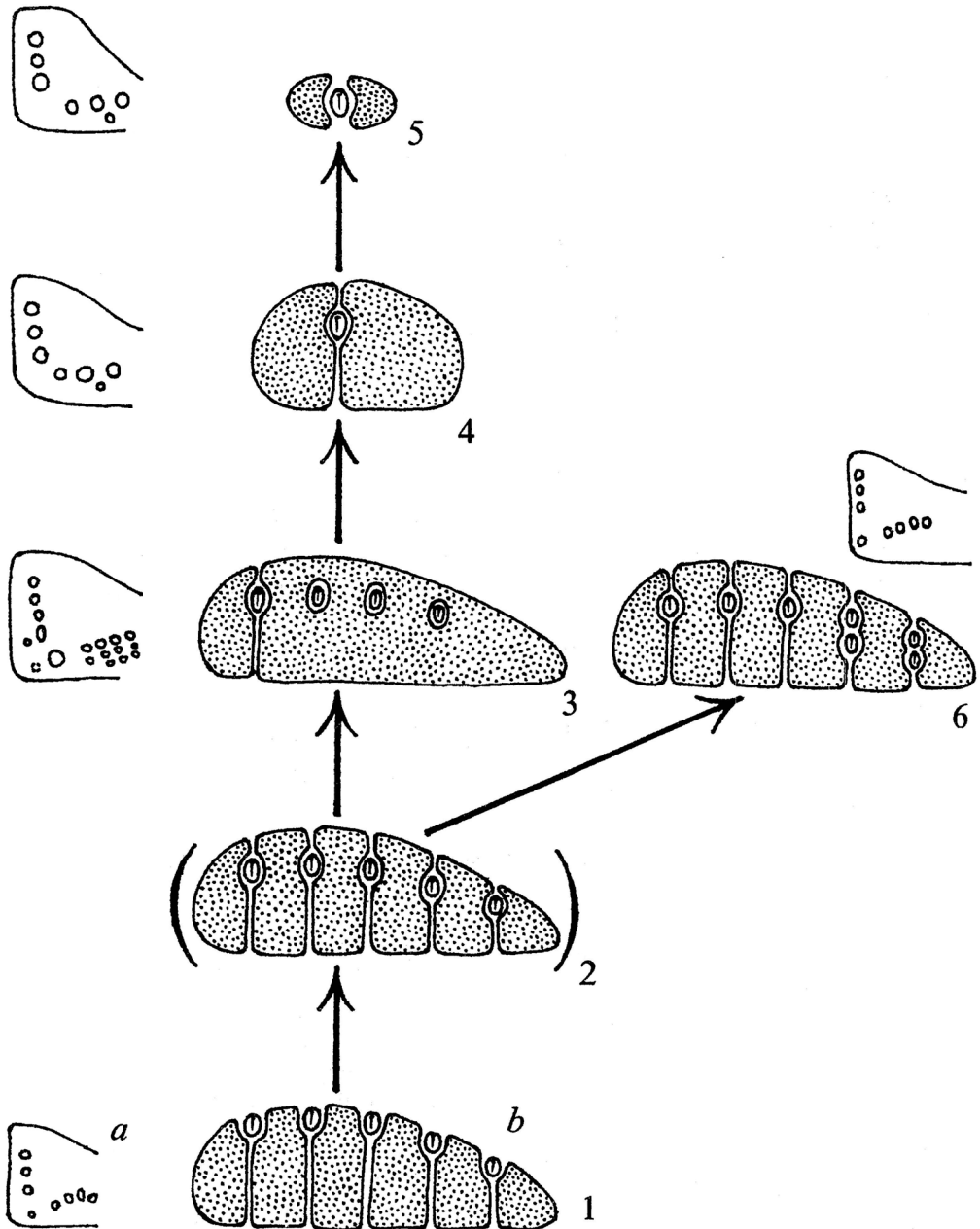


Fig. 19. Transformations of wax-pore plate of abdominal tergite in nymphs of Cixiidae and of sensory pits on medial part of their pronotum (diagrammatic; partially after Yang & Yeh, 1994). 1, plesiomorphic state (many tribes incl. Brixini, Oecleini, Bothriocerini); 2, hypothetical intermediate state; 3, *Kuvera* (Semonini) and some others; 4, *Cixius* (Cixiini); 5, *Ankistrus* (Cixiini) and others; 6, Pentastirini (*Pentastiridius*, *Mnemosyne* and others).

rested on the level of junior instar of Cixiidae, as Wilson's (Wilson & McPherson, 1981; Wilson & Tsai, 1984) data show. The increasing begins from one island in the first instar, each subsequent instar adding one more island. All complementary islands are similar to each other, but differ from the initial one. In the first instar larvae of *Hysteropterum* (now *Agalmatium grylloides* (F.)), Silvestri (1934) showed only one wax-pore on each side of the seventh tergite and normal wax-pore plate on the eighth one, he did not describe other instars.

The larval development of Fulgoroidea has been investigated but slightly. There is much yet to be learned both for morphological and phylogenetic knowledge.

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