Evolutionary Transformations of Abdominal Wax-Plates in the Larvae of the Fulgoroidea (Homoptera, Cicadina)

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Abstract—The main patterns of wax-plates in the nymphs of Fulgoroidea are reviewed in the ontogenetic and phylogenetic aspects. A hypothesis of the common origin of the sensory pits and wax glands of the Fulgoroidea is proposed. The morphological coordination of the sensory pits and wax-glands is discovered. Each elementary wax-plate (wax plaque) is derived from a solitary wax gland, which is associated with a definite sensory pit of the ground plan and regulated by a stable ontogenetic program. Each subsequent instar is characterized by appearance of one additional sensory pit and one elementary wax-plate, arising from one primary wax gland.

In the family Cixiidae the number of wax-islands is equal to that of the corresponding sensory pits (two in the 1st instar, and six in the 5th instar). In the higher Fulgoroidea, the second sensory pit (the first derived one) has no corresponding wax gland. In the 1st instar there are two sensory pits, but one wax plaque corresponds to the first sensory pit. One pit and one wax plaque are added in each subsequent instar. An initial wax gland in the ontogenesis polymerizes into a wax-plate. Polymerization normally starts at the embryonic stage, but in the family Derbidae and in some Tropiduchidae and Issidae, owing to development retardation, the initial solitary wax glands remain in the young instars (Issidae) or in all instars (Tropiduchidae).

The macroevolution of the Fulgoroidea proceeds through the following stages: (1) wax plaques; (2) fusion of elementary plaques into a common secondary wax-plate; (3) detachment of the common wax-plate from tergal sclerotization, with the sensory pits first remaining on the sclerotized portion and subsequently moving to the membrane along the side of the wax-plate.

Wax-plates of the 3 plate-bearing segments (VI–VIII) are arranged in the united vertical hind surface of abdomen, the sclerotizations of tergites VII and VIII become very narrow or disappear. This evolutionary stage is attained in Fulgoridae and Dictyopharidae. The subsequent evolution includes the contrary process of ceasing development of the wax-plates at different intermediate stages, differentiation of different parts of wax-plate into diverse types, and differentiation of plate-bearing segments according to the grade of development and shape of the wax-plates. The wax-plates of segment VI weaken and disappear, while those of segment VII may also weaken (Issidae). Finally, in the families Flatidae and Eurybrachyidae the wax-plates expand onto segments III–V at different ontogenetic stages.

The nymphs of planthoppers of the superfamily Fulgoroidea possess peculiar wax-producing structures termed the wax-plates and formed by clearly localized dense wax glands. Their principal and initial position is on abdominal tergites VI–VIII. In the adults of Fulgoroidea, the wax-plates can be found in several unrelated taxa. They are present only in the females and mostly in positions different from those of the nymphs; direct succession between the nymphal and imaginal plates, i.e., preservation of the larval character in the adult, may be considered only for representatives of Fulgoridae (*Phenax* Germar, *Pterodictya* Burmeister, and *Cerogenes* Horváth). In Meenoplidae and Kinnaridae, belonging to a single phyletic lineage, the wax-plates are present only in the females in the same position as in the nymphs (but not adults) of Cixiidae; however, they are absent in the nymphs of Meenoplidae, while the nymphs of Kinnaridae have not been described. In Cixiidae, the wax-plate is present on the pygophore of females. Planthoppers of the families Lophopidae and Eurybrachyidae have wax-plates on the anal tube and modified lateral lobes of the ovipositor valves.
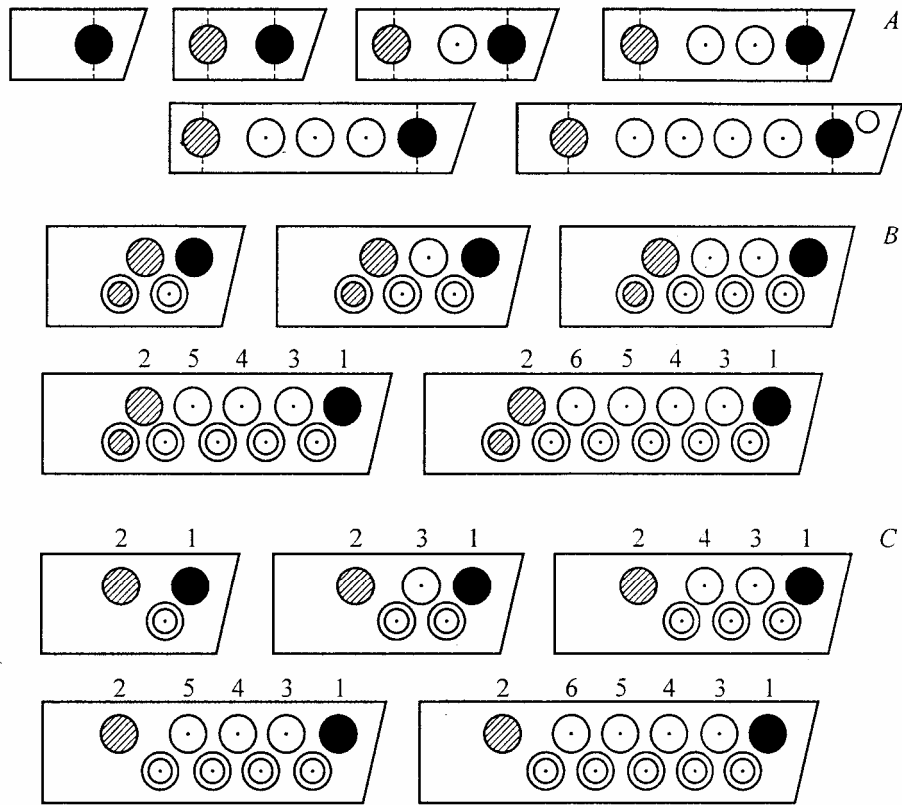
Fig. 1. A generalized diagram of sensory pits and primary (elementary) wax-plates on abdominal tergites in different groups of Fulgoroidea: *A*—Delphacidae: sensory pits are present, wax-plates are absent. *B*—Cixiidae: sensory pits are shown in the upper row, and primary wax-plates, in the lower row. *C*—Flatidae etc., same as in *B*. The sensory pits are numbered according to the sequence of their appearance during development (*1–6*). The diagrams show the right side of tergites VI–VIII.

Judging by the published drawings (Distant, 1906; Melichar, 1915; Soulier-Perkins, 1998), the adults of *Corethrura* Hope (Lophopidae, Lophopini) have wax-plates arranged in the same way as in the nymphs of Eurybrachyidae: the plates are present not only on segments VI–VIII but also on III–V. This fact is very important since it may point at the ancestral group of Eurybrachyidae. However, the material needed to confirm it is currently unavailable to the author.

It is difficult to say at which development stage (adult or nymph) and on what part of the body the first wax-plate appeared in the ancient Fulgoroidea. However, considering the distribution of wax-plates in the recent groups and the fact that the wax glands are closely associated with sensory pits (a nymphal character), they are likely to have appeared on segments VI–VIII of the nymphs, as in Cixiidae. The adaptive significance of the wax-plates probably consists in protection of the integuments from wetting and defense from predators (spiders, etc.), both mechanically and by providing the cryptic effect. In addition, the adults (♀) use the produced wax to cover the egg lay-

ings. The adaptive significance of waxy secretion and structures produced of wax, such as threads or envelopes, is still insufficiently understood. This communication will concern only the evolutionary and morphological transformations of the wax-plates.

The wax-plates of Fulgoroidea became known owing to the works of K. Šulc (1928, 1929) who also studied the numerous and diverse wax glands of scale insects.

A real breakthrough in the study of diversity of wax-plates was accomplished by the group of researchers headed by Chung-Tu Yang (Taiwan). Together with his students (and partly in collaboration with M. Wilson), Chung-Tu Yang described the nymphs of many species from most families of the superfamily Fulgoroidea (Tsaur et al., 1986; Chang and Yang, 1989; Fang, 1989; Wu and Yang, 1989; Yang, 1989; Yang et al., 1989; Cheng and Yang, 1991a, 1991b, 1991c, 1992; Yang and Yang, 1991; Yang and Yeh, 1994, etc.). S.W. Wilson (US) with co-authors contributed much to the study of
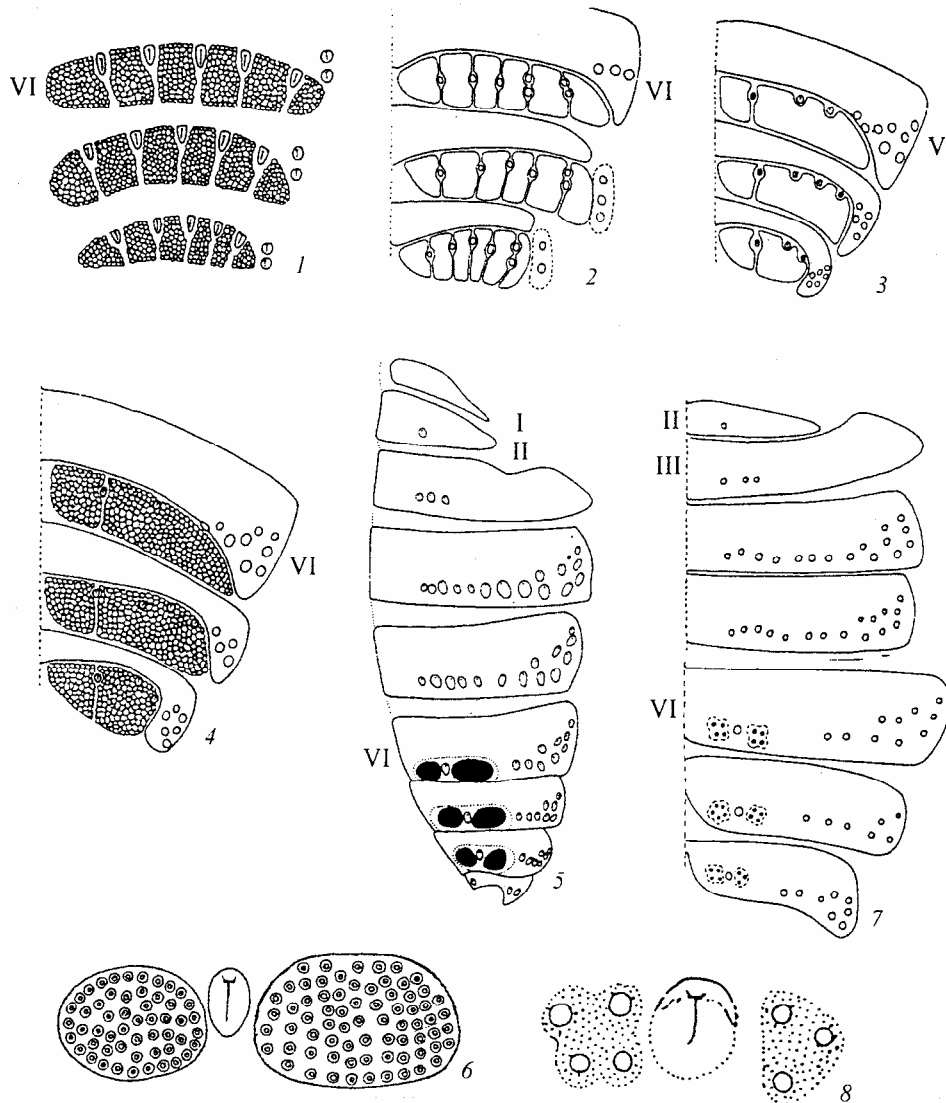
Fig. 2. Family Cixiidae. Wax plates of tergites VI–VIII in *Mundopa kotoshonis* Mats. (*1*); wax plates of tergites VI–VIII in *Oliarus* (s. l.) sp. (*2*), "*Cixius* sp. 2" (*3*), and *Kuvera* sp. (*4*); abdominal tergites I–IX in dorsolateral view (*5*) and enlarged view of wax-plates of *Cixius* sp. (Estonia) (*6*); flattened abdominal tergites II–IX (*7*) and enlarged view of wax-plates of "Cixiini sp. 3" (*8*). *1–4, 7, 8* after Yang and Yeh, 1994; *5* after Emeljanov, 1989; *6* after Šulc, 1928.

the nymphs of Fulgoroidea, especially the nymphal ontogeny (Wilson and McPherson, 1981a, 1981b, 1981c, 1981d; Wilson and Tsai, 1982, 1984; Wilson et al., 1984, etc.). The nymphs of the family Dictyopharidae, mostly the subfamily Orgeriinae, were studied by the author (Emeljanov, 1980, 1993, 1994, 1995, 2001).

Among the lower Fulgoroidea, the wax-plates are absent only in species of the family Delphacidae; in the other primitive family, Cixiidae, the plates are well-developed and probably demonstrate a state close to the initial one (Fig. 1*B*). A V instar nymph has a single row of 5 sensory pits on each side of the ter-

gite[1], closer to the anterior margin; in the gaps behind the pits there is one row of 6 wax-plates (the pits may be positioned close to the posterior margin if there are no wax plates). In each successive instar, one pit and one wax-plate are added to the rows, from the tergite side to the median line; these changes were clearly documented for Cixiidae starting from instar III (Wilson et al., 1984), the total number of instars is 5. By extrapolation, it may be assumed that instar I should have 1 sensory pit and 2 wax-plates (Fig. 1*B*).

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[1] In the descriptions below, the number of pits and wax-plates is given for one side of the body (the right side in the drawings).
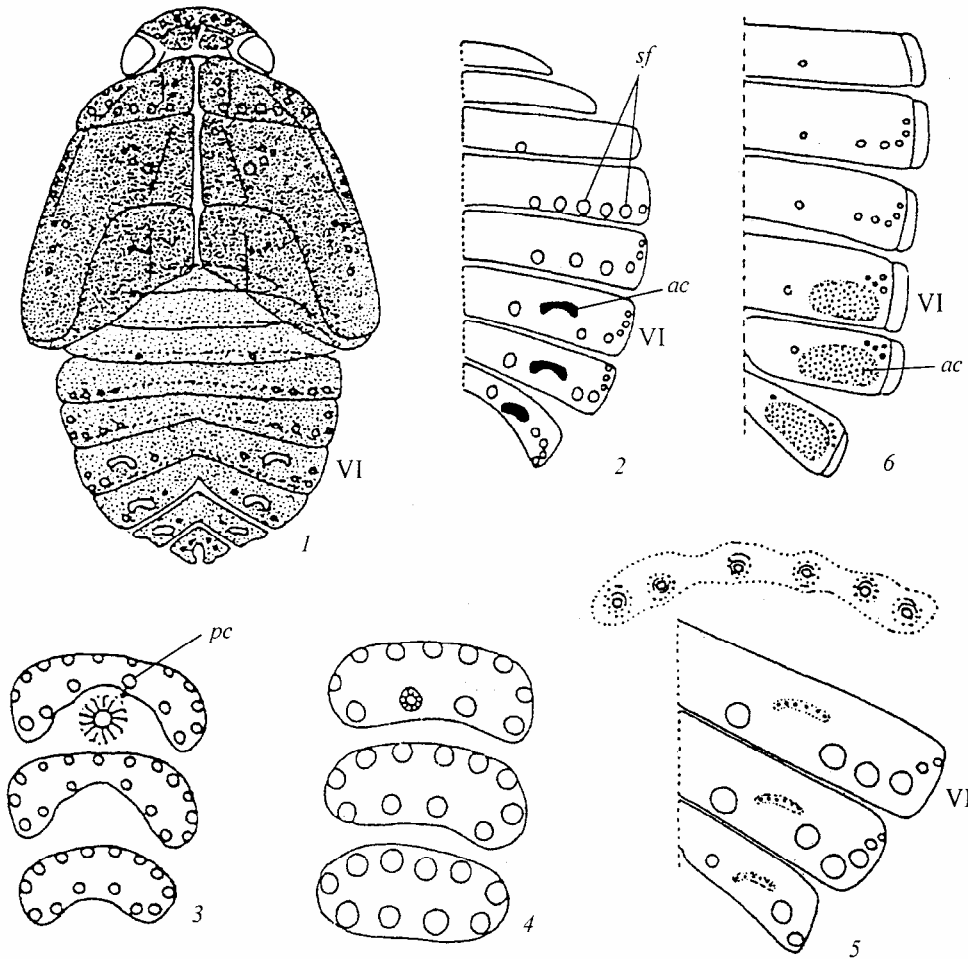
Fig. 3. Family Achilidae. "Achilidae sp. 4" (Plectoderini) (*1–3*): body in dorsal view (*1*), right side of flattened abdominal tergites (*2*), and wax-plates, with an enlarged view of one gland (*3*); wax-plates of tergites VI–VIII in "Achilidae sp. 3" (Plectoderini) (*4*); wax-plates of tergites VI–VIII in *Deferunda truncata* Chen (Plectoderini), with an enlarged view of one plate (*5*); right side of flattened abdominal tergites of *Cixidia fusca* Walker (Achilini) (*6*). After Yang and Yeh, 1994. The Roman numerals designate abdominal tergites (only some of them; mostly tergite VI on which the first wax-plate is located). Other designations: sensory pits (*sf*), separate wax glands (*pc*), and wax-plates (*ac*). Unless otherwise stated, the drawings refer to the last (V) instar nymphs.

Planthoppers of the family Flatidae reveal nearly the same pattern of wax-plate growth from instar to instar (Fig. 1*C*), except for the fact that they have one wax-plate less: the 1st median wax-plate is absent, so that the median sensory pit has no corresponding plaque. In the family Flatidae the complete ontogenetic sequence was documented, starting from instar I (Wilson and Tsai, 1984). The increasing number of sensory pits from instar to instar can be reliably illustrated by the example of the family Delphacidae, in which there are no wax-plates (Fig. 1*A*). In different representatives of Delphacidae, the number of sensory pits on the tergite of I-instar nymphs varies from 0 to 3. If only one pit is present in instar I, as in *Delphacodes nigrifacies* Muir (Calvert et al., 1987), the next pit in instar II appears in a more median position; later, however, the lateral

pit gives rise to the third pit which pushes the second one toward the median line; the third pit gives rise to the fourth pit in the same way, pushing the second pit still further in the median direction.

This process was observed in *Stenocranus lautus* V.D. (Calvert and Wilson, 1986). Each new pit, starting from the third, appears near the lateral pit. Initially it is small and reaches the final size only in the subsequent instar. Thus, the second pit, i.e., the first "derived" one, has a specific status as compared to the third and subsequent pits. Strangely enough, judging by the drawings of S.W. Wilson and J.H. Tsai (1984), the second pit of *Ormenaria rufifascia* Walk. appears only in instar V, whereas all the other pits appear in the usual sequence. It may be assumed that the wax glands (plates) and sensory pits have originated very
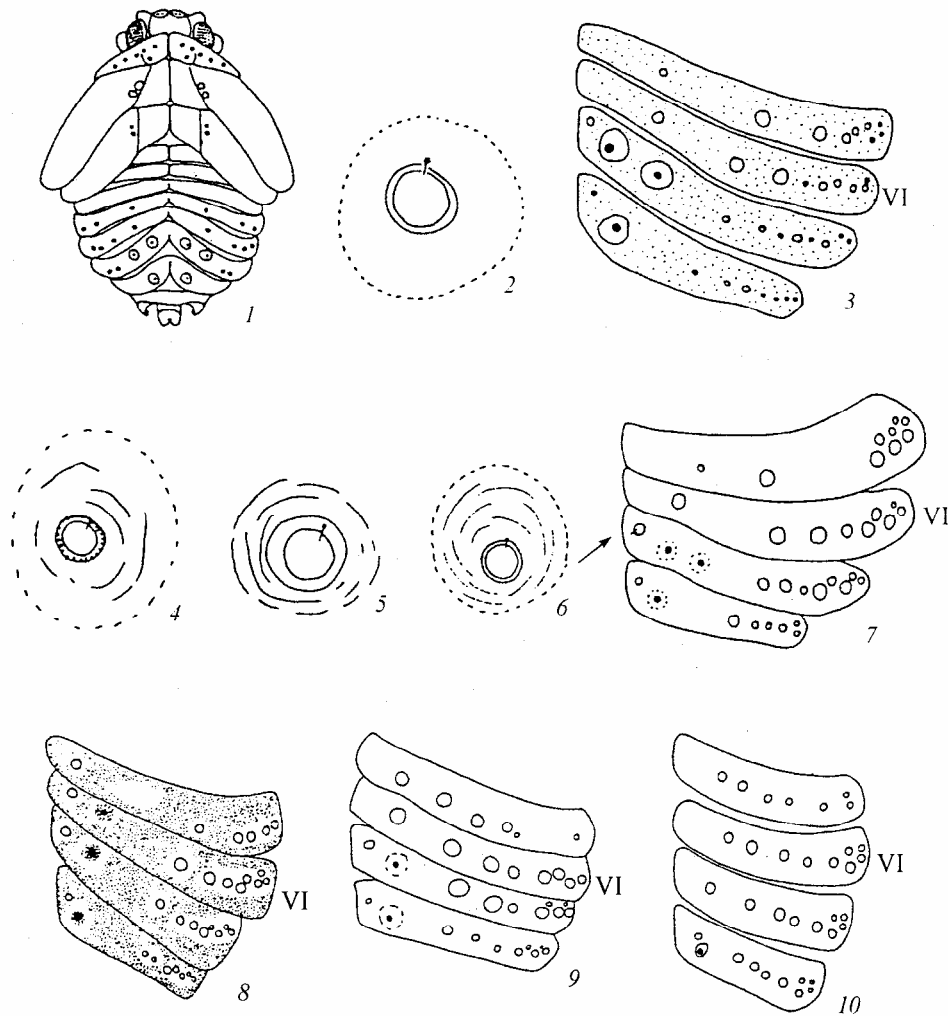
Fig. 4. Family Derbidae. *Muiredusa ignota* (Yang et Wu) (Cedusini) (*1–3*): body in dorsal view (*1*), a separate wax gland (*2*), and abdominal tergites (*3*); a separate wax gland in *Pamendanga matsumurai* Muir (Zoraidini) (*4*), *Saccharodite caudata* Yang et Wu (Rhotanini) (*5*), and *S. acuta* Yang et Wu (*6*); abdominal tergites of *S. acuta* Yang et Wu (*7*), *Basileocephalus germanus* Yang et Wu (Cenchreini) (*8*), *Kaha fruticosa* Yang et Wu (Otiocerini) (*9*), and *Mysidioides nymphalba* Yeh et Yang (Otiocerini) (*10*). After Yang and Yeh, 1994.

long ago from the same initial structure. The sensory pits are formed near setae, which have a similar arrangement on the abdominal tergites in Cicadellidae (Membracoidea) as well. A sensory pit is a special organ (apparatus), apparently providing the sense of humidity in the nymphs of Fulgoroidea. It is shaped as a shallow crater with a seta directed parallel to the integument surface from the crater margin. The sensory pits are usually arranged in rows on the tergal sclerites (Šulc, 1928, 1929; Liebenberg, 1956; Emeljanov, 2000). The erect setae of Membracidae sometimes have craters near their bases, resembling those of the sensory pits (Emeljanov, 2001); on the other hand, the sensory pits also produce wax (Kershaw and Kirkaldy, 1910; Šulc, 1928).

The sensory pits and solitary wax glands of Fulgoroidea have the same origin. The large crater-shaped solitary wax glands, described in the family Derbidae, replace the wax-plates composed of smaller glands. Each gland has a seta positioned at the anterior margin, similar to what is observed in the sensory pits; however, this seta is erect (Figs. 4, *2, 4–6*). The final stage of wax-plate reduction in the family Tropiduchidae is also represented by crater-shaped glands (Fig. 11, *6–9*), whereas the preceding stage is characterized by 3 large glands (homologous to crater-shaped ones) (Fig. 11, *5*) surrounded by the usual small wax glands; this family is discussed below. In the family Issidae, where the wax glands in instar V are present only on abdominal segments VII and VIII, the gland of
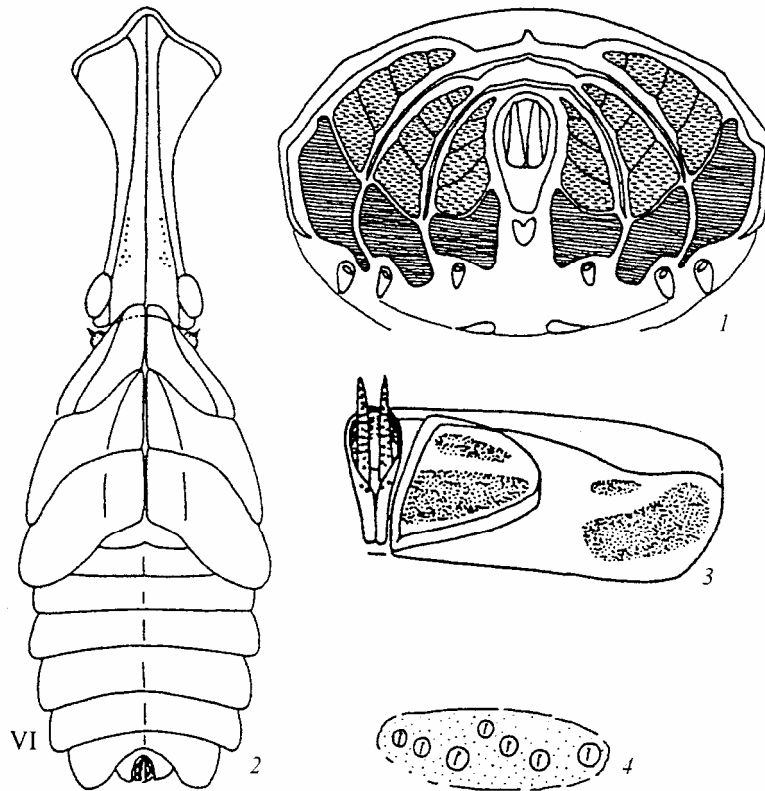
Fig. 5. Family Fulgoridae. *Zanna tenebrosa* F., apex of abdomen in posterior view, starting from segment VI (wax plates of the first type are hatched with broken lines, those of the second type, with solid lines) (*1*); *Pyrops* sp. ("Fulgoridae sp. 2") (*2–4*): body in dorsal view, with sensory pits omitted (*2*), apex of abdomen in posterior view, starting from segment VII (*3*), and laterotergite of segment VIII (*4*). *1*, orig.; *2–4*, after Yang and Yeh, 1994.

segment VII is smaller than that of segment VIII. The first instar nymphs of *Agalmatium flavescens* (Olivier) (= *grylloides* F.) (tribe Issini, subtribe Agalmatiina) have a single crater-shaped gland on tergite VII and a usual plate of simple wax glands on tergite VIII (Fig. 10) (Silvestri, 1934). Although other instars were not described by the cited author, it is clear that at some instar the crater-shaped gland will be replaced by a normal wax plate typical of instar V. The margin of the sensory pit produces wax. In adult planthoppers of the genus *Oliarus* s. l. the wax plates above the ovipositor bear setae or scales (Šulc, 1929).

The family Cixiidae (Fig. 2) demonstrates a series of transformation of the wax-plates (Emeljanov, 2001, 2002). Starting from the initial state (Fig. 2, *1*), the sensory pits shift into the gaps between the plates, the plates merge into a single field, the wax field is reduced, and some sensory pits disappear. The specific morphogenetic status of the median sensory pit (which is present already at instar I) manifests itself in the most peculiar way in the tribes Pentastirini and Semonini. In *Pentastiridius pachyceps* Mats. (Pentastir-

ini) the 1st and 2nd plates merge, while the sensory pit becomes enclosed by the field; on the contrary, in *Kuvera* sp. (Semonini) all the plates become merged and reduced, except for the two median ones which are separated by the median pit. In the tribe Cixiini the reduction of the fields reaches the point where only two median plates and the separating pit are preserved; the plates are reduced in size, and in some genera (*Ankistrus* Tsaur and unidentified representatives of Cixiini) each plate comprises only 3–5 glands (Yang and Yeh, 1994).

The family Cixiidae can be initially characterized by 6 plates and 5 associated sensory pits. In Cixiini 4 lateral plates disappear but the corresponding pits are preserved. The lateral margin of the tergite, or laterotergite, has a pit or a longitudinal row of 2–3 pits which are not associated with wax plates and can be easily discriminated.

The initial sensory pit (shown in black in Fig. 1) also generates pits located on the laterotergite. In the case when the wax-plates are absent and the pits are
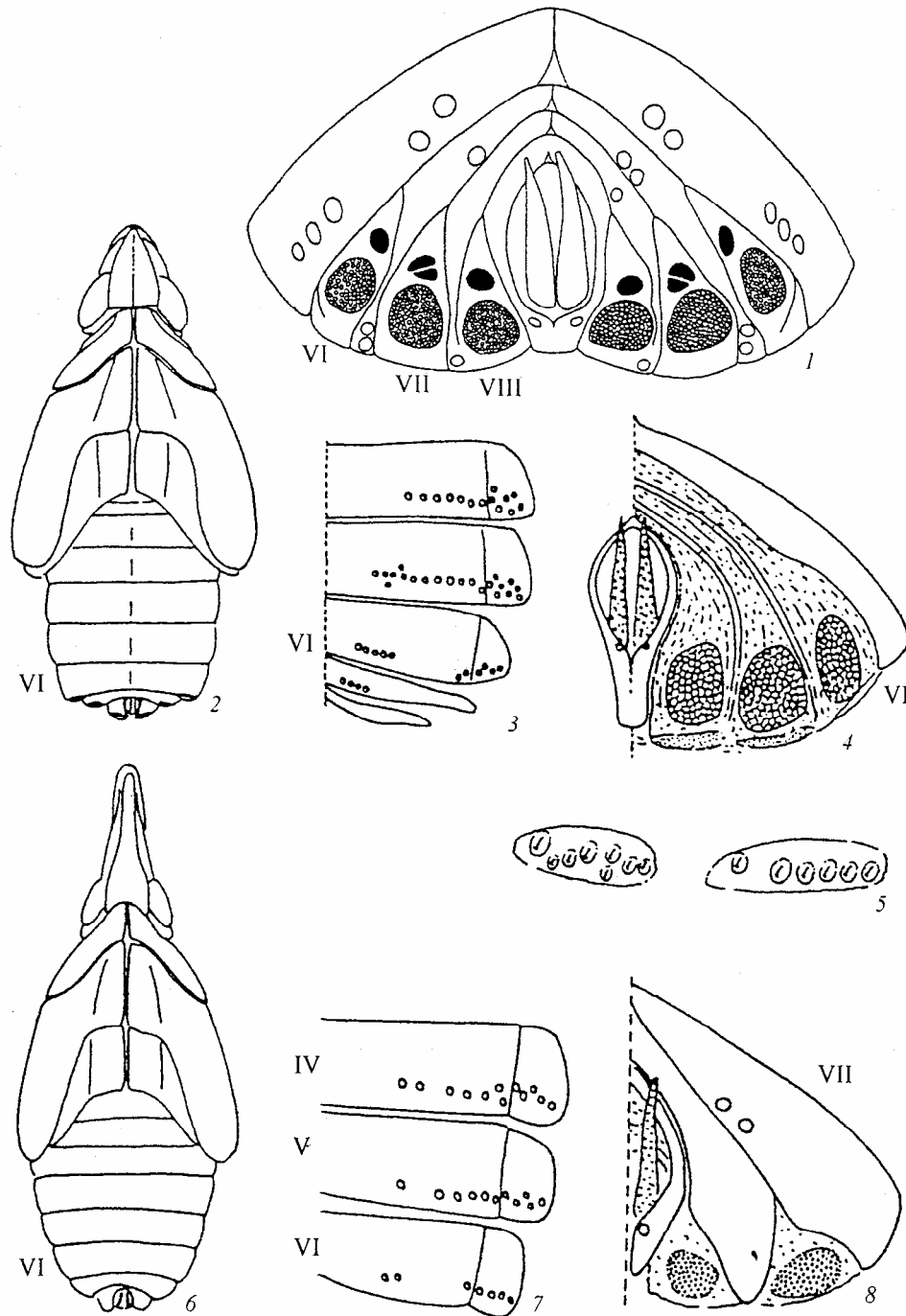
Fig. 6. Family Dictyopharidae, subfamily Dictyopharinae. ?Orthopagini gen. sp., Late Eocene, abdomen in dorso-posterior view, starting from segment VI (*1*); *Orthopagus splendens* Germ. (*2–5*): body in dorsal view, with sensory pits omitted (*2*), flattened abdominal tergites (*3*), apex of abdomen in posterior view, starting from segment VI (*4*), and laterotergites of segments VII and VIII (*5*); *Scolops* sp. (*6–8*): body in dorsal view, with sensory pits omitted (*6*), flattened abdominal tergites (*7*), and apex of abdomen in posterior view, starting from segment VI (*8*). *1* after Emeljanov and Shcherbakov (in litt.); *2–7* after Yang and Yeh, 1994.

located close to the posterior margin, the derived lateral pits (the laterotergal pits) are arranged in a single oblique row directed antero-laterally to nearly longitudinally. If the wax-plates are present, the initial pit and other pits of the tergite proper shift forward, while the derived laterotergal pits become directed laterocaudally to longitudinally. The number of pits on the laterotergite is usually no more than 3.

The next branch up the phylogenetic tree of Fulgoroidea comprises the families Achilidae, Derbidae,
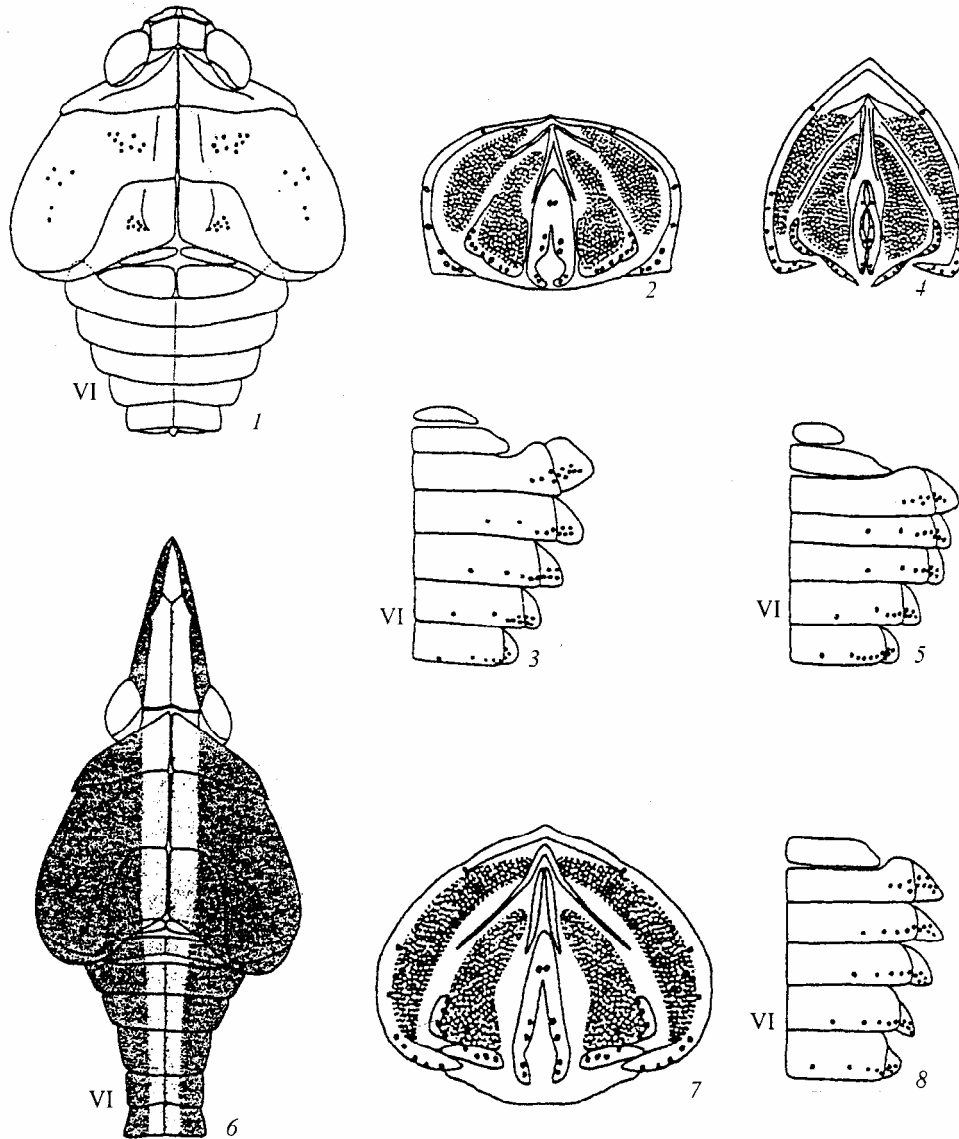
Fig. 7. Family Nogodinidae, subfamily Tonginae. *Ecapelopterum yehynense* Cheng et Yang (*1–3*): body in dorsal view (*1*), abdomen in posterior view, starting from segment VII (*2*), and flattened abdominal tergites (*3*); *E. mirum* Chang et Yeh (*4* and *5*): abdomen in posterior view, starting from segment VII (*4*), and flattened abdominal tergites (*5*); *Tonga westwoodi* Sign. (*6–8*): body in dorsal view (*6*), abdomen in posterior view, starting from segment VII (*7*), and flattened abdominal tergites (*8*). After Yang and Yeh, 1994.

Kinnaridae, and Meenoplidae. The family Achilidae occupies the basal position, and the family Derbidae is derived from the former; these two families, unlike the rest of Fulgoroidea, are characterized by nymphal mycophagy. This lineage also includes the families Kinnaridae and Meenoplidae; the nymphs of the former family have not been described, the nymphs of the latter family have no wax-plates but such plates are present in the adult females (Tsaur et al., 1986). The originally nymphal structure must have been preserved in the adults but lost by the nymphs.

The family Achilidae (Fig. 3) is characterized by wax-plates, which are more expansive in the tribe Achilini and small in Plectoderini; the planthoppers of the tribe Rhotalini have no wax-plates, and the nymphs of other tribes have not yet been described.

A characteristic feature of the nymphs of the family Achilidae and all the families positioned above it on the phylogenetic tree is the absence of the median plate (Fig. 1C); the number of plates is reduced from 6 to 5, and the median pit lies medially to the median wax plate (technically the second one), as in the rest of Fulgoroidea. The remaining primary wax-plates in Achilidae have merged into a single secondary field; the pits surrounded by the wax-plates, i.e., originally located between the plates, have disappeared, while
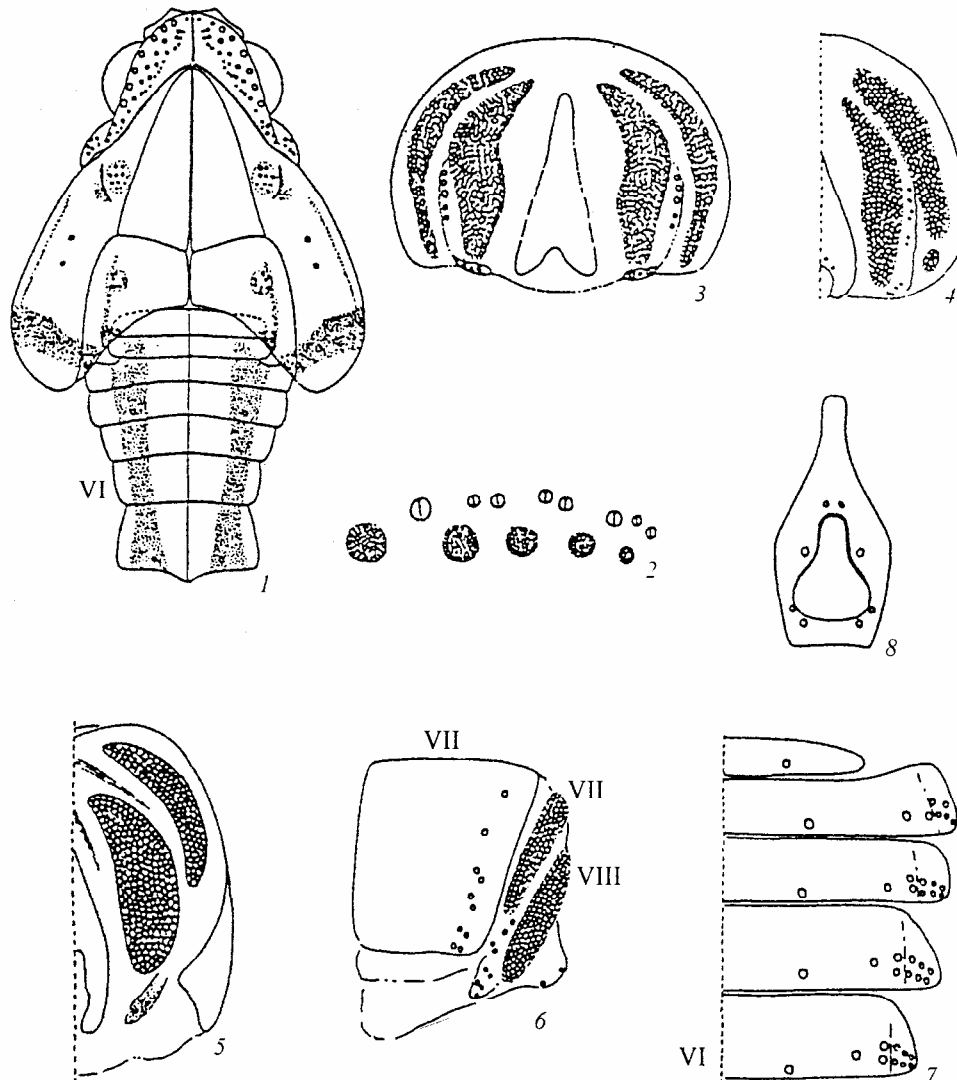
Fig. 8. Family Nogodinidae, subfamily Nogodininae. *Mindura subfasciata* Stål (Varciini) (*1–4*): body in dorsal view (*1*), wax-plates of tergite VI (*2*); abdomen in posterior view, starting from segment VII (*3*), and the same view of a different specimen (*4*); *Pisachu naga* Dist. (Pisachini) (*5–8*): abdomen in posterior (*5*) and lateral view (*6*), starting from segment VII, flattened abdominal tergites (*7*), and segment IX in posterior view (*8*). After Yang and Yeh, 1994.

those not enclosed by the plates have been preserved. The transversely elongated field observed in the tribe Achilini (Fig. 3, *6*) corresponds to the 2–5th primary plates merged together, whereas the sensory pits associated with actual plates are absent. In the tribe Plectoderini (Fig. 3, *1–5*) the field is shorter; it results from the merging of the 2–4th plates. The 2nd and 3rd pits, which would have been pressed between the plates, are absent, while the 4th and 5th pits are present. Thus, one can observe mutual exclusion of the pit and the wax-plate in the achilid lineage. This conclusion is confirmed by similar relations of homologous structures in the derived family Derbidae.

In the family Derbidae (Fig. 4) the initial wax-plates have been reduced, or, more exactly, oligomerized to a single large crater-shaped wax gland per field. Already in Plectoderini (Fig. 3, *3–5*) the number of individual glands in the common field is reduced to 6–12. In Derbidae there are 1 or 2 crater-shaped glands on each side of the tergite and 3 or 2 sensory pits, positioned laterally of them, respectively (Fig. 4, 3, *7–10*).

The next step of the evolution of Fulgoroidea is represented by the sister families Dictyopharidae and Fulgoridae (Figs. 5, 6). More primitive representatives of the family Fulgoridae (genus *Zanna* Kirk., in particular *Z. tenebrosa* F.) have all the 5 wax-plates fully developed (Fig. 5, *1*), whereas in more advanced members of the family the number of plates decreases (Fig. 5, *3*) and the wax fields are gradually reduced starting from segment VI. Among Dictyopharidae, the
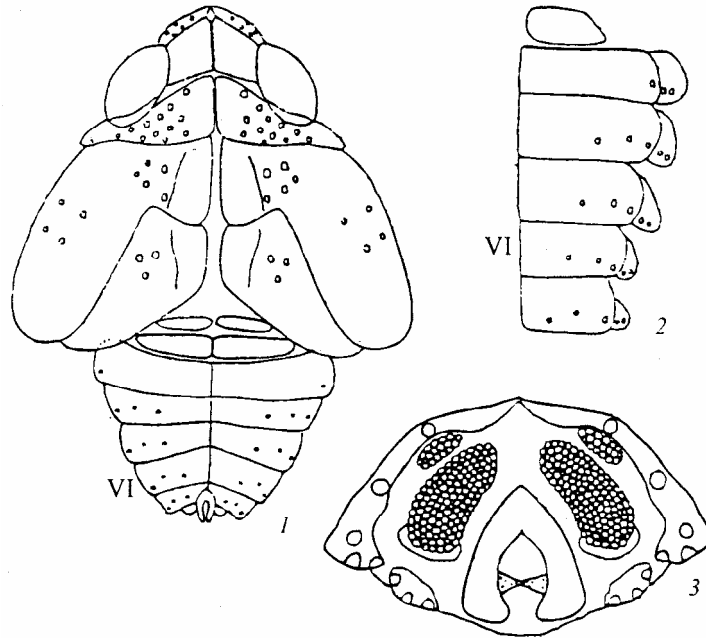
Fig. 9. Family Issidae, tribe Thioniini. *Eusarima astuta* Yang: body in dorsal view (*1*), flattened abdominal tergites (*2*), and abdomen in posterior view, starting from segment VII (*3*). After Cheng and Yang, 1992.

wax fields are present only in the subfamily Dictyopharinae, where they are often reduced on segment VI (Fig. 6, *8*). In the genus *Nersia* Stål, the field of tergite VI disappears during transition from instar IV to V. Planthoppers of the subfamily Orgeriinae have no wax fields (Emeljanov, 1980, 1984). The pair Fulgoridae–Dictyopharidae reveals for the first time differentiation of plates with respect to their secretion and the structure (shape?) of their glands. In *Zanna tenebrosa*, four median plates (the 2–5th) are positioned close together, have the same general appearance, and produce white wax, whereas the 6th plate occupies a more separate position and secretes darker, brownish wax. Members of the family Dictyopharidae have only one large field (lateral or ventral) and a very small cell above it. An Eocenic fossil representative of the family (an amber inclusion) has a small field on segment VII subdivided into two cells positioned closely together (Fig. 6, *1*); they may correspond to the remains of the 1–4th plates present in the nymphs of *Zanna* (Fulgoridae).

The families Fulgoridae and Dictyopharidae show a distinct trend towards reduction of the number and size of wax fields on abdominal segment VI. In some representatives of Dictyopharidae, the fields of segment VI are completely developed at instar I and become gradually reduced or entirely eliminated by instar V; however, most members of his family revealed no such reduction.

The evolution of wax fields in the so-called higher Fulgoroidea (Figs. 7–17) is characterized by a variable combination of differently directed trends. The initial trend consists in reduction of wax fields on segment VI, which therefore becomes similar to the preceding segments. This trend is completely realized in the families Issidae (Figs. 9, 10), Tropiduchidae (Fig. 11), and Lophopidae (Fig. 16). Besides them, there are more families, subfamilies, and tribes showing a complete secondary reduction of wax fields: Caliscelidae, Orgeriinae, Risiinae (Dictyopharidae), Nicertini (Derbidae), Hemisphaeriini (Issidae), and some others. In the families Issidae and Tropiduchidae, segment (tergite) VI is almost identical to the preceding ones. The same phenomenon is observed in Tonginae (Nogodinidae) (sensu Gnezdilov, 2007) (Fig. 7) and some Acanaloniidae (Fig. 12). A small wax field is present on tergite VI of *Acanalonia conica* Say and V instar nymphs of some other species, while *A. viriditerminata* Leth. has no such field (Fig. 12, *2–5*).

The combination of primitive and a priori advanced characters in the morphology of wax-producing abdominal segments (VI–VIII) in the subfamily Tonginae (Nogodinidae) allows one to hypothesize that the ancestor of all the higher Fulgoroidea completely lost (in the phenotype) wax fields on segment VI and retained some primitive sclerotized tergal structures on segments VII and VIII. In more advanced representatives these structures were reduced, but at
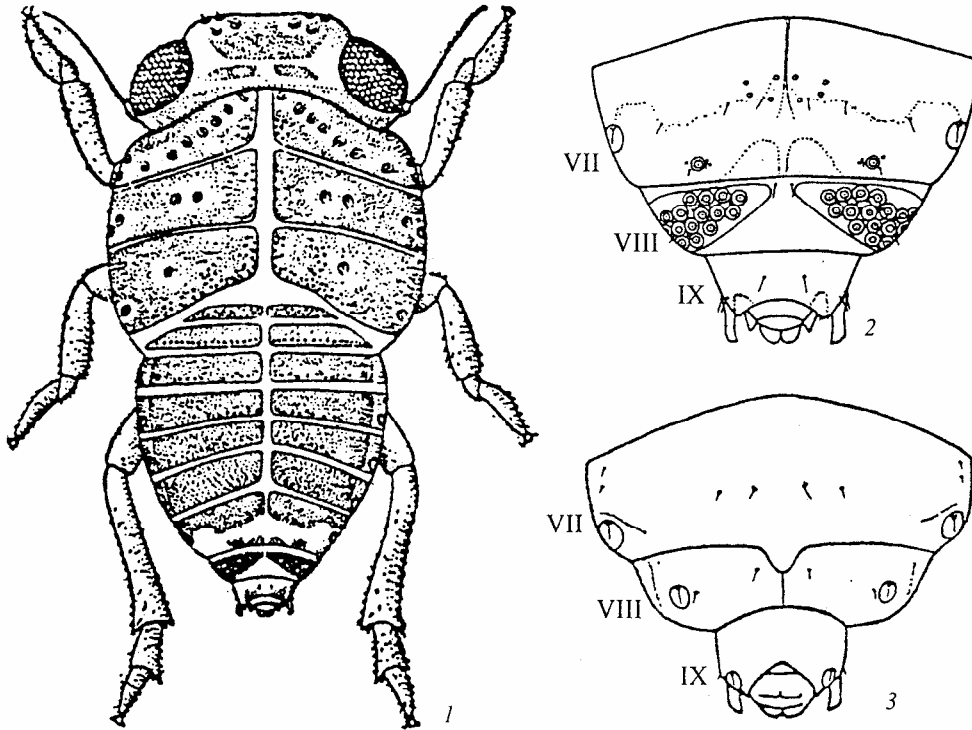
Fig. 10. Family Issidae, tribe Issini. *Agalmatium flavescens* Olivier, I instar nymph: body in dorsal view (*1*), apex of abdomen starting from segment VII in dorsal (*2*) and ventral view (*3*). After Silvestri, 1934.

the same time the wax fields on segment VI were restored.

The reappearance of wax glands on tergite VI can be explained by the ontogenetic development of these glands, which was described above on the material of Cixiidae (Fig. 1*B*). The I instar nymphs have a single wax plaque (plate); then, with every instar, one new plate and one sensory pit are added laterally to the existing ones but medially to the lateral pit (demonstrated in *Ormenaria*). An increase in the number of pits may be accompanied by transformation of the entire wax field, namely membranization of the periphery of the wax plaques and change of their orientation from horizontal or oblique to vertical, at an angle to the tergite (the tergite is membranized from the chain of sensory pits to the posterior margin). The turn on the wax fields into the vertical position is observed in the nymphs of Dictyopharinae (and evidently Fulgoridae) during the transition from instar III to IV (Emeljanov, 1980). However, already in Kinnaridae and Meenoplidae (but in the adults) the fields are positioned vertically at an angle to the tergites; the same phenomenon was observed at instar V of Pentastirini (Cixiidae), but the exact timing of the turn of wax fields in development of Cixiidae was not documented.

In V instar nymphs of Flatidae (Fig. 14) and Nogodinidae (Fig. 8, *2*) the plaques on tergite VI were observed to lie in the plane of the tergite; some Tropiduchidae appear to have only 1 plaque (Fig. 11, *4*, *6*). The next phase of differentiation, namely the shift of the plaques (plates) onto the membrane, is observed in the families Ricaniidae (Fig. 13) and Eurybrachyidae (Fig. 17); however, in these families the associated sensory pits are also positioned on the membrane. The last phase, namely the merging of separate plates into a common field, similar to what is observed on segments VII and VIII, is typical of Eurybrachyidae (Fig. 17, *3*, *4*). The reversion here is almost complete.

Tergite VI demonstrates a complete morpho-cycle (Emeljanov, 2000) consisting of several states that correspond to different phases of ontogenetic integration–disintegration of wax plates, reflecting the evolutionary steps from a uniform gland to a common field. The morpho-cycle includes the following stages.

(1) A complete suppression of the plaques.

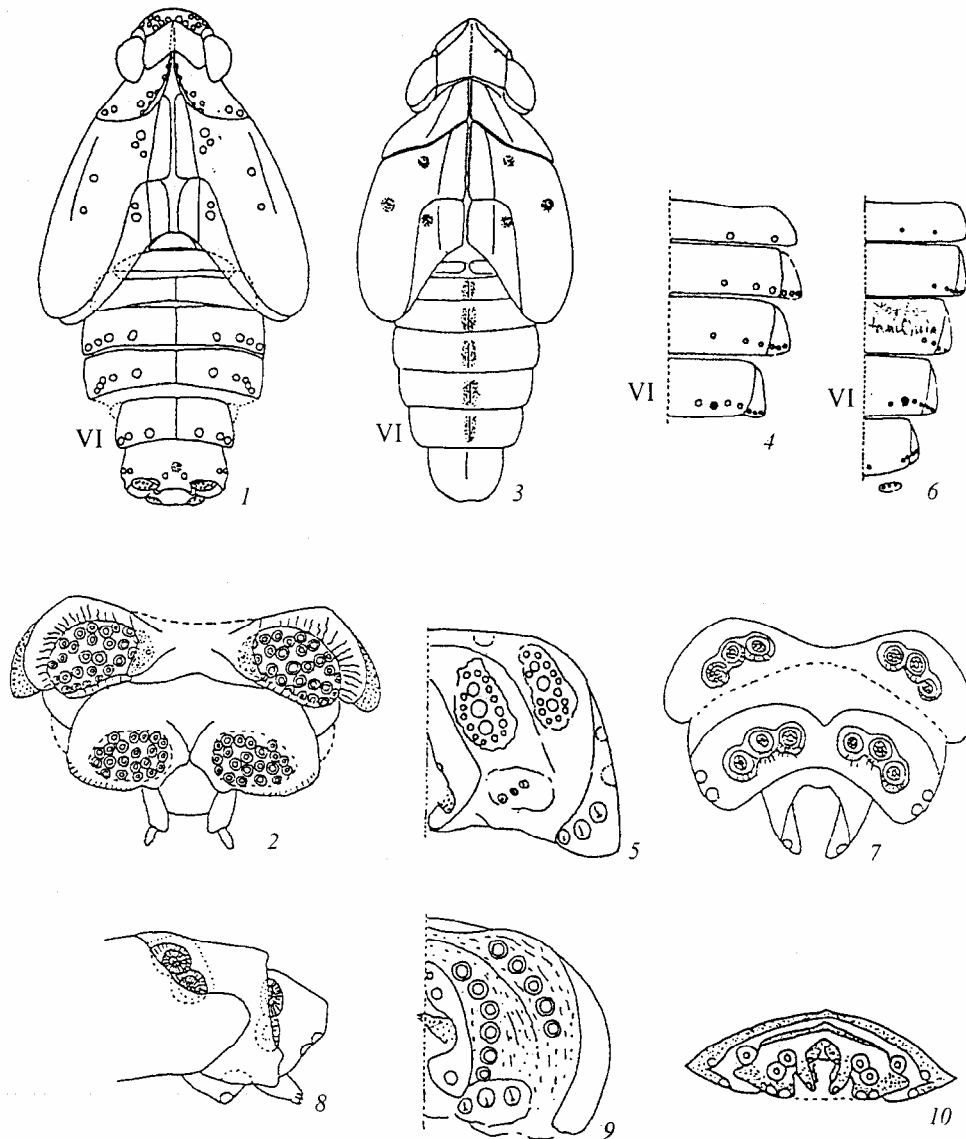(2) Expression of the plaques and suppression of differentiation.

Fig. 11. Family Tropiduchidae. *Catullia subtestacea* Stål (Catulliini) (*1*, *2*): body in dorsal view (*1*) and apex of abdomen in dorso-posterior view, starting from segment VII (*2*); *Mesepora onukii* Mats. (Eporini) (*3–5*): body in dorsal view, with sensory pits omitted (*3*), flattened abdominal tergites (*4*), and apex of abdomen in posterior view, starting from segment VII (*5*); *Leptotambinia viridinervis* Kato, flattened abdominal tergites (*6*); *Ossoides lineatus* Bierm. (Tambiniini), apex of abdomen in dorso-posterior view, starting from segment VII (*7*); *Kallitaxila sinica* Walk. (Tambiniini), apex of abdomen in lateral view (from the left), starting from segment VII (*8*); *Neommatissus formosanus* Kato (Neommatissini), apex of abdomen in posterior view, starting from segment VII (*9*); *Lanshu glochidionae* Yang, Yang et Wilson (Tambiniini), apex of abdomen in posterior view, starting from segment VII (*10*). *1–7*, *9* after Yang et al., 1989; *8* after Yang and Yang, 1991.

(3) Expression of differentiation without merging (i.e., suppression of merging).

(4) A complete expression with merging.

The morpho-cycle is made more complicated by the presence of the sensory pits.

The transformations of the wax-plates of segments VII and VIII are to a considerable degree correlated and largely similar to those of segment VI. Tergite VIII is partly or completely desclerotized. In the primitive state its median half is sclerotized (Nogodinidae, Flatidae); later, sclerotization remains only in the form of laterotergite (Acanaloniidae, Issidae, Tropiduchidae); then the laterotergal sclerotization disappears but the pits remain (some Flatidae, Lophopidae); finally, the pits also disappear (Ricaniidae, Eurybrachyidae).

The initial state of the wax-plates on segments VII and VIII is characterized by large, uniform, entire
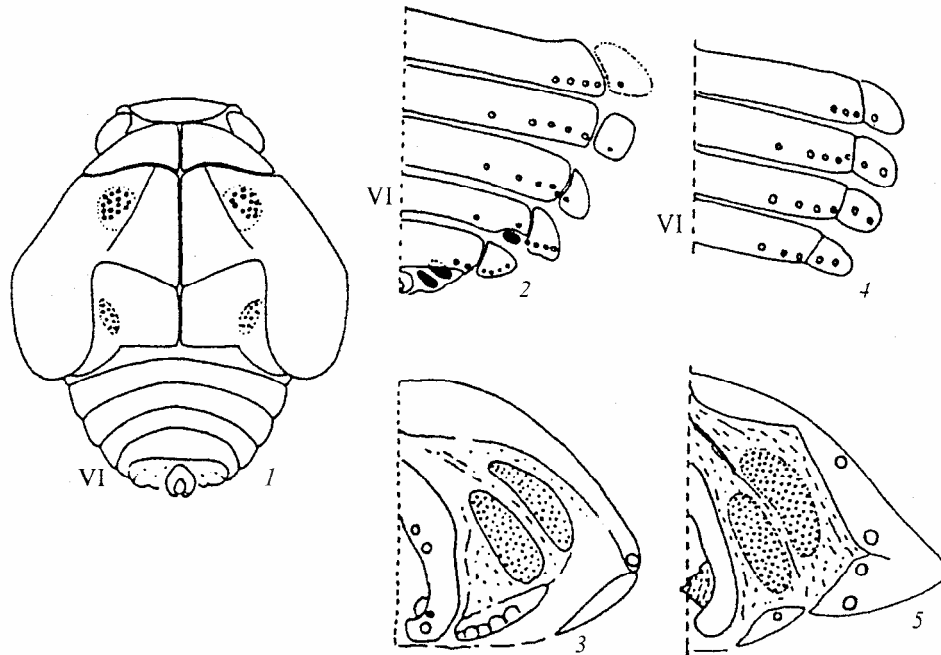
Fig. 12. Family Acanaloniidae. *Acanalonia conica* Say (*1–3*): body in dorsal view (*1*), flattened abdominal tergites (*2*), and apex of abdomen in posterior view, starting from segment VII (*3*); *A. viriditerminata* Leth. (*4*, *5*): flattened abdominal tergites (*4*) and apex of abdomen in posterior view, starting from segment VII (*5*). After Yang and Yeh, 1994.

plates, observed in Nogodinidae, Acanaloniidae, and Ricaniidae (segment VIII); the plates are reduced in the families Issidae and Tropiduchidae, in Issidae more essentially on segment VII, whereas in Tropiduchidae the plates are gradually reduced, the number of elementary wax glands decreasing to 1 on segment VII (Fig. 11, *10*); in the families Ricaniidae, Flatidae, and Eurybrachyidae the common fields disintegrate partly (Ricaniidae) or completely into individual plates or plaques (some Eurybrachyidae: see Fig. 17, *8*); in Ricaniidae disintegration is evident only on segment VII, where the two lateral plates are separated, giving the impression that the factor impeding differentiation becomes weaker in the caudal direction.

In the families Flatidae, Lophopidae, and Eurybrachyidae the fields of wax glands are divided into two parts: the median (dorsal) field is separated and differs in the structure (size) of the elementary wax glands, while the remaining 4 fields have identical glands; the primary plates (plaques) may be clearly delimited or merged with no traces of boundaries.

Thus, it may be assumed that at the first stage of transformation of wax-producing apparatus of the posterior abdomen the wax-plates on tergite VI were suppressed, at the second stage the suppression was weakened and segment VI acquired the status similar to that of segments III–V, preserving at the same time

the potentials typical of segments VI–VIII. The last essential transformation of wax-producing apparatus was its expansion onto segments V–III, following the pattern of segment VI on the phase of "plaques on membrane," observed in some representatives of Flatidae and Eurybrachyidae (Figs. 14, *6*, *9*; 17, *3*, *4*, *6*, *7*). This phenomenon was previously referred to as metatopy (Emeljanov, 1987), i.e., placement of a structure into a different position, in this case onto different segments. In one species of the family Eurybrachyidae, described by Chung-Tu Yang and Wen-Bien Yeh (1994), the common pattern of wax-plates expanded onto tergite VII (Fig. 17, *5*) and even tergite VIII (Fig. 17, *8*). The spreading of wax-plates over the entire abdomen and their differentiation by the type of glands and the wax produced obviously have a certain, still unknown, adaptive significance.

Based on the transformations of the wax apparatus described above, the families of planthoppers can be arranged in a certain morphological series, even though the position of the families Acanaloniidae, Issidae, and Tropiduchidae cannot be defined with absolute certainty.

The morphological series of transformation of the wax producing apparatus, reflecting the main pathway of its evolution, is very important from the phylogenetic viewpoint, since the schemes based on other
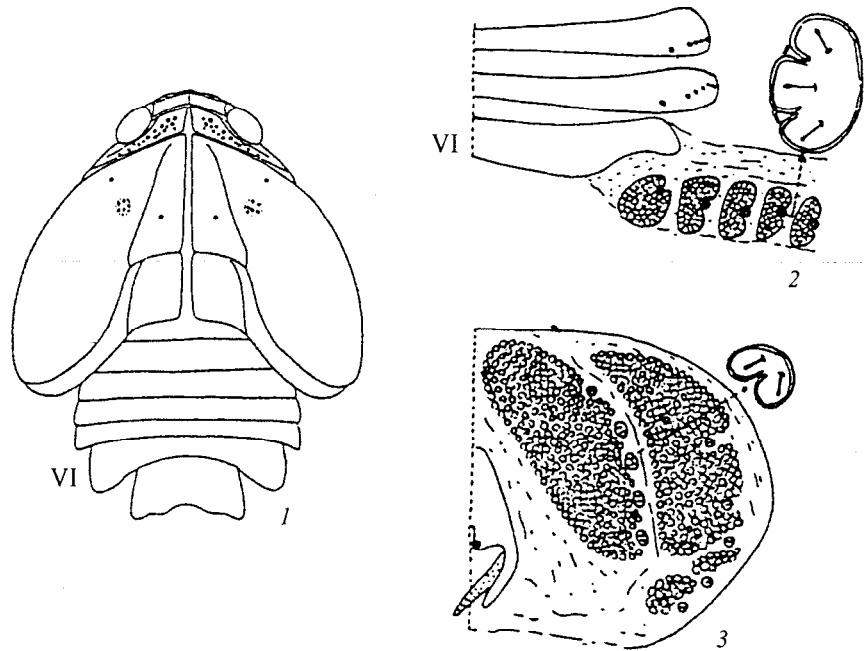
Fig. 13. Family Ricaniidae. *Ricanula sublimata* Jac. (*1–3*): body in dorsal view (*1*), flattened abdominal tergites (*2*), and apex of abdomen in posterior view, starting from segment VII (*3*). The bipartite and tripartite sensory pits are shown separately in *2* and *3*. *1* after Yang, 1989; *2* and *3* after Yang and Yeh, 1994.

characters cannot adequately resolve the phylogenetic relationships of the higher Fulgoroidea.

The development trends of the lower Fulgoroidea lead to a complete disappearance (in the phenotype) of wax glands on segment VI and to elongation of segment VII. Some species of the family Nogodinidae, especially the subfamily (or tribe?) Tonginae and the tribes Pisachini (*Pisacha* Dist.) and Varciini (*Mindura* Stål) most strongly resemble the hypothetical ancestor of the higher Fulgoroidea. They have complete and uniform wax-plates. The pits are located on sclerotized parts of both tergites, sclerotization of segment VIII is strongly reduced but still the most complete as compared to that of other representatives of the higher Fulgoroidea. The lateral part of the tergite forms a single structure with the laterotergite, the tergite proper has 5 pits, and the laterotergite, 3 pits; tergites VII and IX show a similar number and arrangement of the sensory pits: $1 + 2 + 3$ and $1 + 2 + 2$.

The primary pits, initially located in front between the wax-plates, are often polymerized (mostly to 3) and may shift into the gaps between the plates (Fig. 2, *2*). In the family Ricaniidae the process of pit polymerization has stopped at an intermediate stage, producing compound craters with two or three setae and a common outline (Fig. 13, *2*, *3*). The elongated tergite lies in front of the wax field; the laterotergite is

longitudinally elongated and lies laterally of the wax field, i.e., in the primitive position. Later, the laterotergite separates from the tergite while the tergite shifts laterally and assumes a longitudinal position. In the family Issidae (Thioniini) tergite VIII in a lateral position looks as a collar of the wax field and has no sensory pits.

The group of planthoppers with complete undifferentiated wax-plates also includes Issidae, Acanaloniidae, and Tropiduchidae. The tergal sclerotization of segment VIII disappears together with the sensory pits (in Issidae the sclerite is still present, but the pits have already disappeared).

Some species of the family Acanaloniidae (only the genus *Acanalonia* was studied) have a small wax-plate on tergite VI, surrounded by a membrane (Fig. 12). This state, resembling that of some members of Dictyopharidae, appears to be the result of a reversion, since the structures of segments VII and VIII closely resemble those of Tropiduchidae and Issidae, but not Nogodinidae. The wax-plate of segment VII is reduced in size in the family Issidae. A I instar nymph of *Agalmatium flavescens* (Olivier) (Fig. 10), judging by the drawing of F. Silvestri (1934), has a wax-plate on segment VIII and only a crater-shaped wax gland on segment VII. In the family Tropiduchidae (Fig. 11) the wax-plates are either noticeably diminished in size or
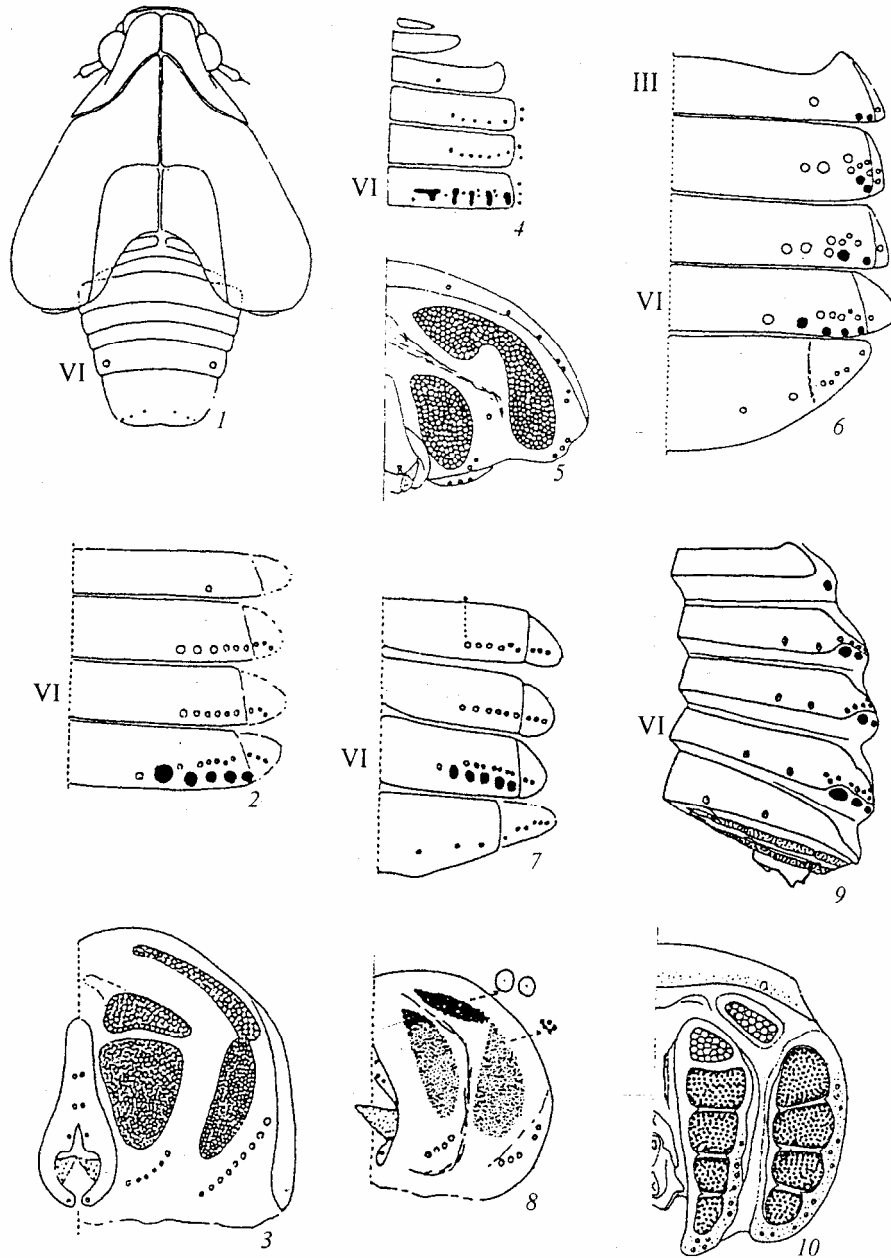
Fig. 14. Family Flatidae. "Flatidae sp. 2" (*1–3*): body in dorsal view (*1*), flattened abdominal tergites (*2*), and abdomen in posterior view, starting from segment VII (*3*); *Anormenis chloris* Mel. (*4*, *5*): flattened abdominal tergites (*4*) and apex of abdomen in posterior view, starting from segment VII (*5*); *Salurnis formosana* Jac., IV instar, flattened abdominal tergites (*6*); *Ormenaria rufifascia* Walk. (*7*, *8*): flattened abdominal tergites (*7*) and apex of abdomen in posterior view, starting from segment VII (*8*); *Phromnia marginella* Oliv. (*9*, *10*): abdomen in lateral view (*9*) and apex of abdomen in posterior view, starting from segment VII (*10*). *1–8* after Yang and Yeh, 1994; *9* and *10* after Šulc, 1929.

reduced to several crater-shaped glands, as in *Agalmatium flavescens* (Issidae) on segment VII, or as in the family Derbidae. The diminished wax-plates have few glands. In *Catullia* Stål all the glands are the same, whereas in *Leptotambinia* Kato, *Mesepora* Mats., and *Sogana* Mats. there are 3 larger glands in the center surrounded by numerous smaller glands. The next phase of oligomerization is characterized by the pres-

ence of only isolated crater-shaped glands arranged in a single transversal row like the sensory pits. Such glands are present in the number of 5–6 (*Ommatissus* Fieb., *Neommatissus* Muir) or 2–3. In the genus *Lanshu* Yang, Yang et Wils. there are 2 pits on segment VII and only 1 pit on segment VIII. In the oligomerized representatives of Tropiduchidae, the presence of 5–6 crater-shaped wax glands appears to be
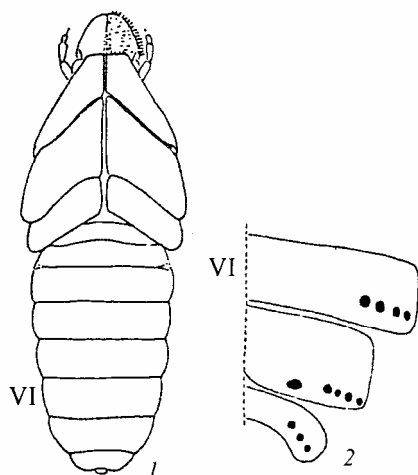
Fig. 15. Family Hypochthonellidae. *Hypochthonella coeca* China et Fenn.: body in dorsal view (*1*) and flattened abdominal tergites (*2*). After Yang and Yeh, 1994.

a derived condition in relation to 3 glands, since the intermediate stage of oligomerization is characterized by 3 large glands surrounded by smaller ones.

The example of *Agalmatium flavescens* suggests that every single wax-plate (plaque) was phylogeneti-

cally derived by polymerization of a single crater-shaped gland. In ontogenesis, the single gland phase is in most cases passed during the embryonic stage; however, in case of extreme oligomerization it may shift back onto the nymphal stage, affecting either only the younger instars, or the entire nymphal period up to the imaginal molt.

Another lineage, also originating from Nogodinidae (Tonginae), comprises the families Ricaniidae, Flatidae, Lophopidae, and Eurybrachyidae. In this phylogenetic line the tergal sensory pits are positioned on the membrane near the wax-plates.

In the family Ricaniidae (Fig. 13) differentiation of the wax-plates by the type of wax glands is not yet evident. However, the lateral part of the wax field has already started disintegrating into primary plates, and 1 or 2 plates have become separated (Fig. 13, *3*). The plates that appear at IV and V instars do not merge.

Another specific feature of this family is the presence (appearance or restoration) of wax fields of segment VI in the form of 5 independent plates separated by sensory pits (Fig. 13, *2*). The wax field of tergite VI
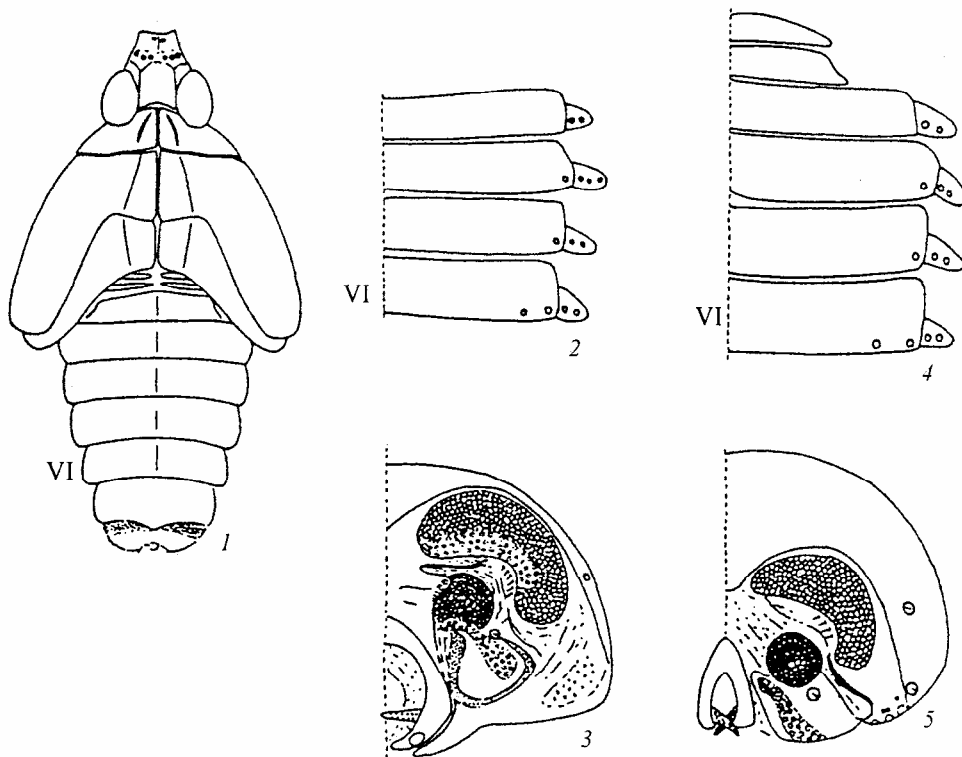

Fig. 16. Family Lophopidae. *Lophops carinata* Kirby (*1–3*): body in dorsal view, with sensory pits omitted (*1*), flattened abdominal tergites (*2*), and apex of abdomen in posterior view, starting from segment VII (*3*); *Elasmoscelis perforata* Walk. (*4*, *5*): flattened abdominal tergites (*4*) and apex of abdomen in posterior view, starting from segment VII (*5*). After Yang and Yeh, 1994.
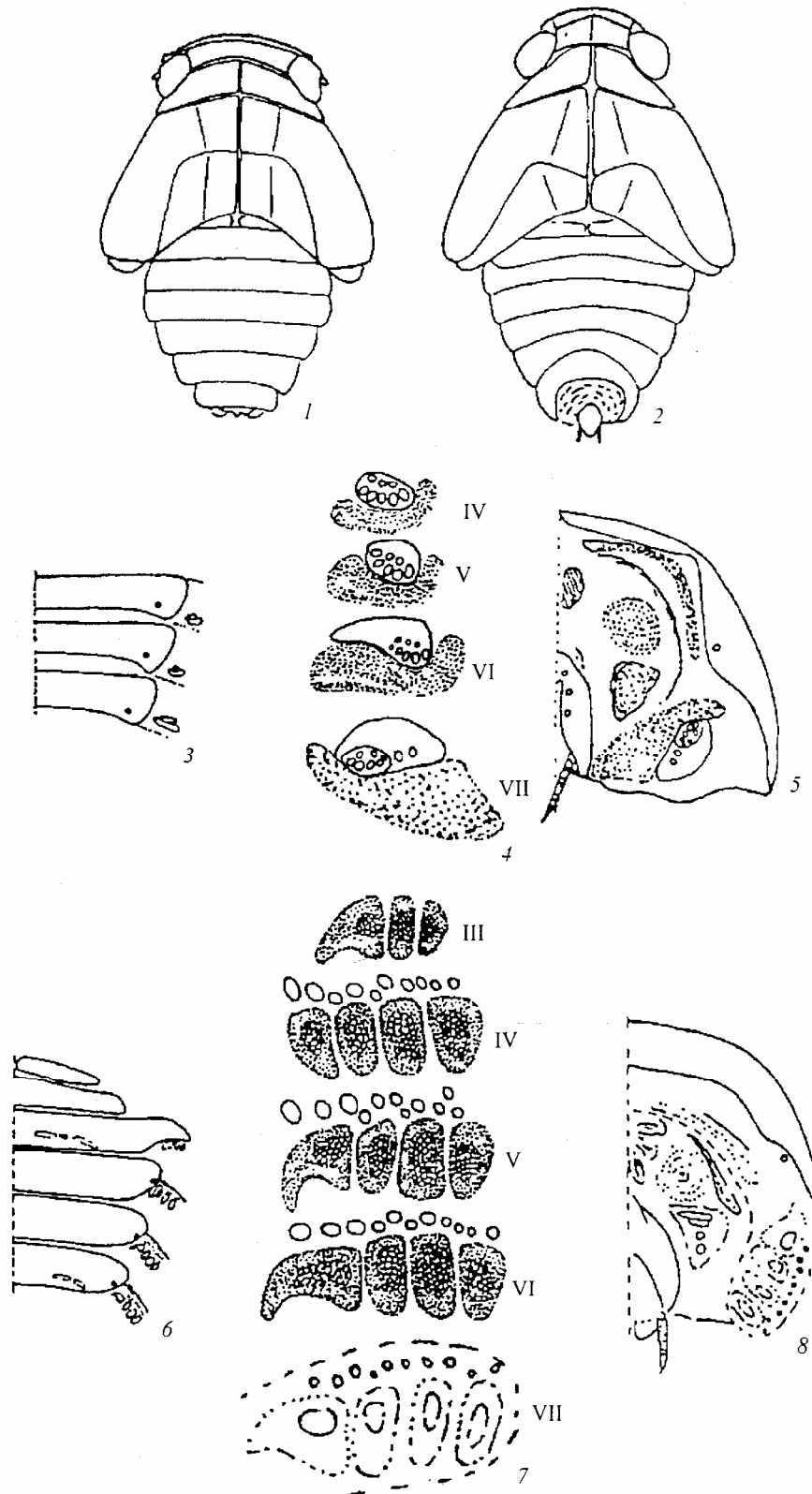
Fig. 17. Family Eurybrachyidae. "Eurybrachyidae sp. 2," body in dorsal view, with sensory pits omitted (*1*); "Eurybrachyidae sp. 1" (*2–5*): body in dorsal view, with sensory pits omitted (*2*), flattened abdominal tergites (*3*), wax-plates of tergites IV–VII (*4*), and apex of abdomen in posterior view, starting from segment VII (*5*); "Eurybrachyidae sp. 2" (*6–8*): flattened abdominal tergites (*6*), wax-plates of tergites III–VII (*7*), and apex of abdomen in posterior view, starting from segment VII (*8*). After Yang and Yeh, 1994.

does not form a common surface with the two following fields but is shifted forward by a distance equal to the length of tergite VII. This feature may be interpreted as an indication of reversive (instaurational) origin of this field, since in Dictyopharidae and Fulgoridae (Zanninae) the fields of all the three segments form a common transversal field.

The family Flatidae (Fig. 14) is characterized by differentiation of the common wax field of tergites VII and VIII into the upper (median) and lower (lateral) plates; the upper plate corresponds to the median plaque (the 2nd plaque in the total order: see Fig. 1*C*), and the lower plate corresponds to the 2–5th (3–6th) plaques merged together with no traces of boundaries left. The separation of the upper plate is also observed in the families Lophopidae and Eurybrachyidae and may represent a synapomorphy of these two families and Flatidae. The correspondence between the lower plate and 4 primary plaques can be illustrated by the example of *Phromnia* Stål (Fig. 14, *10*), in which the plaques have distinct boundaries. Tergite VI in Flatidae mostly has 5 primary plaques positioned on the sclerotized part of the tergite (Fig. 14, *2*, *4*, *7*). This typical and possibly primitive state of wax fields is correlated with the absence of fields on anterior abdominal segments. However, there are 2 interesting exceptions to this rule (Fig. 14, *6*, *9*): in IV instar of *Salurnis formosana* Jac. (V instar is unknown) tergites III–V bear 2 plaques each, identical to the plaques of tergite VI where they are present in the number of 4 (Yang and Yeh, 1994); in *Phromnia marginella* Oliv. (Šulc, 1929) the plates corresponding to the plaques are positioned on the membrane, even though the sensory pits, unlike in Ricaniidae, remain on the sclerite (Fig. 14, *9*); segments III–V bear 1, 2, and 3 plates, respectively, whereas segment VI has 3 rather than 4 plates.

It may be assumed that the ancestors of Ricaniidae and Flatidae diverged at the stage at which the plaques were positioned on the sclerite, and that their plaques independently shifted onto the membrane. This process was accomplished only in part of the family Flatidae (the system of this family is still far from perfect). Neither *Salurnis* Stål nor *Phromnia* Stål can be regarded as a primitive representative of the family.

In some species of the family Flatidae (demonstrated in *Ormenaria rufifascia* Walk.) the field of segment VIII has not yet been divided into 2 parts (or these parts have secondarily merged together?), although the glands are clearly differentiated into upper and the lower type. If subdivision into the upper and lower parts in Flatidae takes place during nymphal development (which is quite likely), then *Ormenaria* demonstrates a case of development retardation.

The very peculiar monotypic group Hypochthonellidae (Fig. 15) should probably be regarded not as a separate family but as an aberrant larvalized subfamily within Flatidae. The nymphs of *Hypochthonella coeca* Ch. et Fenn. have no sensory pits on all tergites, including the three wax-producing ones (VI–VIII); their wax glands are represented by primary plaques in the number of 4, 5, and 3, respectively.

The two remaining families, Lophopidae (Fig. 16) and Eurybrachyidae (Fig. 17) share a unique synapomorphy in the morphology of their wax plates: the glands of the upper (median) field are arranged in regular concentric circles (Yang and Yeh, 1994; Soulier-Perkins et al., 2006; Soulier-Perkins, 2008)[2]. The sister-group relations between Lophopidae and Eurybrachyidae have been demonstrated using other characters as well (Emeljanov, 1990; Urban and Cryan, 2007). The members of Lophopidae have no wax fields on segment VI or any preceding segment (with the possible exception of the genus *Corethrura* Hope, as mentioned above), whereas in Eurybrachyidae wax fields are present on membranes of all the tergites where they can be formed, i.e., tergites III–VIII (segments I, II, and IX are strongly modified).

Only two representatives of the family Eurybrachyidae, not identified to genus, have been studied (Yang and Yeh, 1994). The fields of segments III–V and VI are similar in both forms, and in one representative ("Eurybrachyidae 2") the lower (lateral) group of plates on segment VIII is largely similar to those of the preceding segments, approaching the state of secondary homonomy. Thus, expansion of wax-plates onto the anterior abdominal tergites of Eurybrachyidae was

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[2] These fields with concentric rows of glands produce a dense bundle of wax threads. In nymphs of the genus *Maana* Soulier-Perkins (Lophopidae), a pair of such bundles evidently imitates antennae of some insect (possibly a cerambycid beetle), producing the impression of a "false head" on the posterior body end (Soulier-Perkins et al., 2006). Imitation of a head on the posterior body end is a widespread phenomenon among insects and other animals, for example fishes. The case of Lophopidae (genus *Maana*, see Bourgoin et al., 2006) is peculiar in that the antennae are imitated by bundles of wax threads and the similarity is enhanced by the presence of pale rings on the threads. It should be noted that the annulated appearance of the bundle requires periodic changes in the composition of wax produced.

accompanied by increasing similarity between the lateral fields of tergites VII–VIII and those of tergites VI–IV, i.e., the loss of previously achieved integration observed in the more primitive groups (Flatidae, Ricaniidae, etc.). Tergites III and VI of "Eurybrachyidae 2" also have the median wax fields on the sclerites, which are, however, similar in shape to the field of segment VII positioned on the membrane. The morphogenetic signal for differentiation of segments III–VIII, which were homonomous in the common ancestor of Rhynchota, appears to be completely blocked in this species.

The proposed scheme of evolutionary transformations of wax-plates in Fulgoroidea is a preliminary one, because our knowledge of the nymphs of many families is still very limited. However, the available material is sufficient to demonstrate the complicated nature of these transformations, which cannot be explained from the viewpoint of a linear evolution.

ACKNOWLEDGMENTS

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