

Larvae – a key to evolution of Culicoidea (Diptera) in the Mesozoic

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ABSTRACT

Fossil records of Culicoidea and history of study of Mesozoic Chaoboridae is reviewed. Chaoboridae played an important role in many Jurassic and Early Cretaceous freshwater assemblages of Asia and research of their very diverse Mesozoic larvae is necessary for any phylogenetic conclusions. Peculiarities of known larvae of *Hypsocorethra toficola* (J₃), *Chironomaptera scobloi* (J₃) and *Mesocorethra levis* (J₃/K₁) are figured and discussed. Several characters unknown in larvae of living chaoborids were discovered in Mesozoic ones, the most interesting is the mouthparts with numerous labral filaments, as in Culicidae, presumably adapted for filter-feeding (new taxon will be described later).

KEY WORDS: Culicoidea. Chaoboridae. Fossil record. Mesozoic. Larvae. Feeding mode.

MODERN CULICIDS

The nominate family of culicoids – Culicidae is possibly one of the best-known groups of the whole class Insecta due to its medical significance and economic importance. Other members of this superfamily Dixidae, Chaoboridae and Corethrellidae, are not so popular but very interesting in phylogenetic respect. Dixidae is the most primitive (but specialized) culicoid family, with their larval morphology and life mode being least advanced than those of other culicoids (Monchadsky 1936): parts of larval body not fused as in other families (3 thoracic segments, 10 abdominal segments, two parts of stigmal plate); amphibiotic larvae feeding on microorganisms and decayed organic material on surface film and non-feeding adults.

In all other families of this superfamily immature stages are fully aquatic: many of them inhabit near water surface (Corethrellidae, most of Anophelinae, chaoborid *Eucorethra*) but others gradually shift deeper and become plankton or bottom feeders (the rest of chaoborids, Culicinae). The feeding modes of Chaoboridae and Culicidae appear to be basically different: in Culicidae proteins are necessary only for adults (their larvae are filter-feeding or scraping of vegetation), in Chaoboridae – for predatory larvae (modern exceptions in both families are secondary).

Now Culicidae is the most flourishing family of the superfamily (38 extant genera with 3200 species are known – Harbach & Kitching 1998), other families: Dixidae (7 extant genera with about 175 extant species; Peters 1989), monotypic Corethrellidae (1/62; Borkent 1993) and Chaoboridae (6/50; Borkent 1993) - are not so diverse. However in the Mesozoic one can see a different picture.

CULICOIDEA IN THE MESOZOIC

In spite of intensive research of Triassic assemblages during the last years (Krzeminski & Krzeminska 2003,

Blagoderov *et al.* 2007), Culicoidea is still not recorded from the Triassic, and no undoubted ancestral forms for any culicoid family are described yet (Lukashevich 1996a). In the earliest Jurassic of Eurasia (Lower Jurassic of Kyrgyzstan and Germany), where the Diptera already is one of important orders, finds of Culicoidea are very scanty and represented only by adult Dixidae and Chaoboridae (Lukashevich 1996a, Ansoerge 1996). Dixidae are very rare in Mesozoic fossil faunas – up to now only two genera (6 species) are described based on 20 specimens from Europe and Asia. Corethrellidae and Culicidae are known only since the Cretaceous and described from two Mesozoic inclusions each: the oldest species of *Corethrella* Coquillett, 1902 is known from Early Cretaceous Lebanese amber and the second species from mid-Cretaceous Burmese amber (Szadziewski 1995, Poinar & Szadziewski 2007); two extinct genera of Culicidae are found in Burmese and Canadian ambers (Poinar *et al.* 2000, Borkent & Grimaldi 2004). Culicidae became numerous later, in the Cenozoic (Edwards 1923): for example in Oligocene Beds of the Isle of Wight (Bembridge Marls) which fossils insects were recently studied in detail Chaoboridae were not found at all, but culicid adults are numerous (more than hundred specimens) and diverse.

It is worth mentioning that chaoborids did not play important role in taphocoenoses of several famous Mesozoic Lagerstätten (Daohugou, Karatau, Shara-Teg, Purbeck and Weald), where dipterofaunas were diverse but conditions for burial of immature stages were unfavourable due to different reasons. However, in many Jurassic and Early Cretaceous freshwater assemblages of Asia, they have flourished, and their immature stages and/or adults were buried in innumerable thousands. It is well-known for Lower Cretaceous deposits of China and Mongolia (e.g. Kalugina 1986, Zhang 1990), where first Mesozoic chaoborids were described from (see below). Sometimes in Jurassic localities of Siberia the Chaoboridae also is the

most numerous family among not only Diptera but total insects (Kalugina & Kovalev 1985, Kalugina 1993, Lukashevich 1996b – Tabl.1).

locality	age	Insecta	Diptera	Chaoboridae
Novospasskoye (Transbaikalia)	J _{1/2}	3100	1961	1800
Uda (Transbaikalia)	J ₃	1470	1244	1150
Khotont (Mongolia)	J ₃ /K ₁	2000	948	587
Manlay (Mongolia)	K ₁	2090	1502	1498
Myangad (Mongolia)	K ₁	4355	1197	1146

Table 1. Number of specimens from selected localities (collections of Paleontological Institute, Moscow).

So it is a pity that in a comprehensive compendium of Grimaldi & Engel (2005) Culicoidea appear only near the Jurassic/Cretaceous boundary on the phylogenetic tree of Diptera (fig. 12.25) and the oldest family Dixidae is recorded since the Cretaceous. By the way, the first Dixidae are shown bloodsucking, but I know no argument for this point of view except for supposition that Culicoidea were primarily bloodsucking and so the oldest family must have such mode of life. Unfortunately, the authors did not discuss this novelty at all. Moreover, according to this cladogram, Chaoboridae are absent during all the period of their Asiatic empire: they presumably originated only in the mid-Cretaceous time as a sister-group of the Culicidae – a thin line indicates the absence of phantom midges in the fossil record. This is a certain mistake.

F.W. Edwards wrote (1923: 153): “The origin and phylogenetic history of the Culicidae must go back well into the Mesozoic Era; and, from the small size and fragile nature of the insects, it is probably too much to hope that we can ever obtain much direct palaeontological evidence on these matters”. Just in 1923 the first Mesozoic chaoborid fossils were described from the Lower Cretaceous of China as larvae of Odonata (Grabau 1923), and the next year a second species was described from the Lower Cretaceous of Mongolia as Chironomidae (Cockerell 1924). Several years later (Ping 1928) the former species was also transferred to Chironomidae, and the first genus was established for fossil chaoborids, *Chironomaptera* (named “chironomid without wings”, because of their rarely preserved wings). Only in 1974 Kalugina proved their affinity to Chaoboridae and established a separate family but later she lowered its status to the subfamily in Chaoboridae (Kalugina 1974, 1977). Up to date 15 described extinct genera are valid, two times more than extant: *Gedanoborus* Szadziewski & Gilka, 2007 from Eocene Baltic amber and 14 genera from Mesozoic deposits:

Astrocorethra Kalugina, 1986
Baleiomyia Kalugina, 1993
Chachotosha Lukashevich, 1996
 “*Chaoborites*” Kalugina, 1985
Chaoburmus Lukashevich, 2000
Chironomaptera Ping, 1928
Dixamima Rohdendorf, 1964
Helokrenia Kalugina, 1985
Hypsocorethra Kalugina, 1985
Mesochaoborus Zhang, Zhang, Liu & Shanguan, 1986
Mesocorethra Kalugina, 1993
Praechaoborus Kalugina, 1985
Rhaetomyia Rohdendorf, 1962
Taimyborus Lukashevich, 1998

Surely it is not the final number and revision of the family is necessary, but now it is premature because of lack of knowledge on too many characters (especially of immatures) of many described genera: descriptions of only six genera are based on different developmental stages and numerous specimens: *Astrocorethra*, *Chachotosha*, *Chironomaptera* (several species), *Hypsocorethra*, *Mesocorethra* and *Praechaoborus*.

CHAOBORID LARVAL DIVERSITY AND CULICID ORIGINS

Up to now described Mesozoic wings of Culicoidea didn't make clear relationships between the families: only dixid *Syndixa* Lukashevich, 1996 with chironomid tendency in venation (Lukashevich 1996a) and chaoborid *Chaoburmus* with corethrellid peculiarities can be mentioned (Lukashevich 2000). Usually the venation is useless even for diagnostics being unified and quite modern; only Mesozoic Dixidae and several Chaoboridae can be distinguished from modern ones by wings, but only in proportions of vein sections, not in venation pattern. Mesozoic immature stages, known only for phantom midges, especially larvae, turned to be more diverse, peculiar and so more useful for future phylogenetic analysis, demonstrating unusual combinations of usual features as well as unknown peculiarities. Now in any comprehensive phylogenetic analysis features of immatures play an important role, e.g. in data matrix for evaluation of phylogeny of Culicomorpha (Saether 2000) larval peculiarities are the most numerous (45 of 81 characters).

The question about the origin of Culicidae is very interesting and often discussed. Borkent & Grimaldi (2004: 887) considered “possible that some Jurassic and/or Cretaceous taxa presently placed in the Chaoboridae, and which are known only as adults, are actually early lineages of Culicidae with short mouthparts... We suggest that culicid-like larvae were present in the Jurassic but the odds of finding these as fossils is unlikely. Culicidae larvae are restricted to small, fishless bodies of water and are therefore unlikely

to be preserved in the lake sediments that characterize the Jurassic freshwater fossil record”.

In the modern fauna only *Chaoborus* Lichtenstein, 1800 inhabits lakes and ponds (sometimes it is considered an autapomorphy of this genus; Saether 1992), the rest being found in puddles, wells and various temporary or permanent fishless pools (Saether 1972). However, hundreds of impressions of chaoborid immatures mean that in the Jurassic – Early Cretaceous all these midges inhabited lakes (some of them presumably fishless – see Kalugina 1977), and maybe the lake was a primary type of chaoborid habitat in the Mesozoic. The same can be true for Culicidae as well, and one has a chance to find immatures of true mosquitoes if they are existed in those times.

Chaoboridae comprise six extant genera (four of them monobasic), differing in their larval morphology and feeding strategies. The only exception in this predaceous family is the filter-feeder *Australomochlonyx* Freeman, 1962. Among others, *Eucorethra* Underwood, 1903 is the surface predator, which specializes on capturing terrestrial insects that land or fall onto the surface of the water. Remaining four genera live in plankton and feed on copepods, cladocerans, dipteran larvae (including cannibalism) by means of their unique prehensile antennae with blade-like apical setae (known elsewhere only in Corethrellidae, but biomechanical principle is different in the latter). The most specialized and successful predator, extant *Chaoborus* is the only cosmopolitan genus. It possesses highly advanced transparent larva with strongly elongate head, approximated antennae, two pairs of conspicuous air sacs, plumose setae of anal fan, and no siphon (never comes to surface). It had been shown that the main event in evolution of Chaoboridae was the shift of their larvae to predation (Monchadsky 1936).

Let's analyze larval morphology in several Mesozoic genera of Chaoboridae, trying to understand their feeding modes and to find in the Jurassic either the early lineages of Culicidae (as proposed by Borkent & Grimaldi 2004) or some culicid traits in chaoborid larvae (Kalugina 1977). Fortunately, in several localities vast material is preserved and numerous structural details can be traced in different species. It is necessary to stress that the author is not a cladist and accept paraphyletic taxa as no less natural than holophyletic ones (Rasnitsyn 1996).

Praechaoborus tugnicus Kalugina, 1985 (Novospas-skoe, J₁₋₂ of Transbaikalia). Prior to their formal description, larvae of *P. tugnicus* were reported as highly advanced and very similar to *Chaoborus* (Kalugina 1977). Later they were shown to be different from *Chaoborus* at least in the shape of head (not so elongate, nearer to *Cryophila* Bergroth, 1930; Kalugina & Kovalev 1985: 70); the presence of air sacs is very questionable and they are not mentioned in description (all impressions are of poor preservation and show little details). So the similarity of *Praechaoborus* to *Chaoborus* is quite doubtful.

Chachotosha Lukashevich, 1996 (Khotont, J₃/K₁ of Mongolia) is as far as we know the earliest chaoborid repre-

senting the *Chaoborus* larval morphotype: transparent larvae with strongly elongate head, approximated antennae, two pairs of prominent air sacs, plumose setae of anal fan, and no siphon. However, according to the several adult and pupal features, *Chachotosha* was distinct from *Chaoborus*, though the ecological niche of its larvae was surely just the same (for details see Lukashevich 1996b). Therefore, it is groundless to synonymize any extinct genus with *Chaoborus* based on any character of fossils, which is now restricted to *Chaoborus* (as proposed by Saether 1992 for *Chironomaptera* due to plumose setae of its anal fan), because more character combinations existed in the Mesozoic than nowadays, including co-occurrence of such characters that are not met together in extant genera.

For instance, now only pupae of *Chaoborus* possess swollen thoracic horn with apical papilla. However, in the Mesozoic one can see pupal horns of the same structure in various genera, both with *Chaoborus*-type larvae (*Chachotosha* – Lukashevich 1996b) and with larvae of a different morphotype, more plesiomorphous without doubts (*Hypsocorethra*; reticulate surface of thoracic horn and even the non-dilated tracheal duct could be traced, the latter was known only in pupae of *Chaoborus* – Fig. 1E).

Hypsocorethra toficola Kalugina, 1985 (Uda, J₃ of Transbaikalia – Figs 1, 2). When the genus was described, Kalugina noted that its broad, dorsoventrally flattened head with widely separated antennae (and we can add, the large submentum, and mentum with apical teeth) is very similar only to the head of *Eucorethra* (Kalugina & Kovalev 1985: 74, fig. 34). So the conclusion was made that *H. toficola* was likewise the surface predator. However, other well-preserved specimens allowed us to find significant differences from *Eucorethra*: typical prehensile antenna with long robust setae not shorter than shaft, mandibular fan, and numerous labral filaments. Two latter groups of setae are absent in *Eucorethra* (considered as apomorphies of this genus – Saether 1992: trend 10); mandibular fan is well-developed in all remaining chaoborids, but labral filaments seem to be not so numerous in extant genera. A decrease in filament number to at most 9 pairs, not divided into two brushes, is considered to be an apomorphy of the family compared with Culicidae where a pair of brushes is usually formed by numerous setae (Saether 1992: trend 11). Nine pairs are very convenient for distinguishing Chaoboridae from Culicidae, because the mouth-brushes composed of only ten stout flattened bristles placed in a regular row are known in culicid *Toxorhynchites* Theobald, 1901 (Edwards 1932).

However, the material studied by Saether was scarce, and he probably did not know a detailed paper of Monchadsky (1939) on larvae of *Cryophila* where this number was shown to vary from 9 to 12. In this extant genus the hydrostatic apparatus is imperfect, so *Cryophila* can not wait for its prey remaining motionless as *Mochlonyx* Loew, 1844, so the former is not so successful predator as the latter (Monchadsky 1939, 1959).

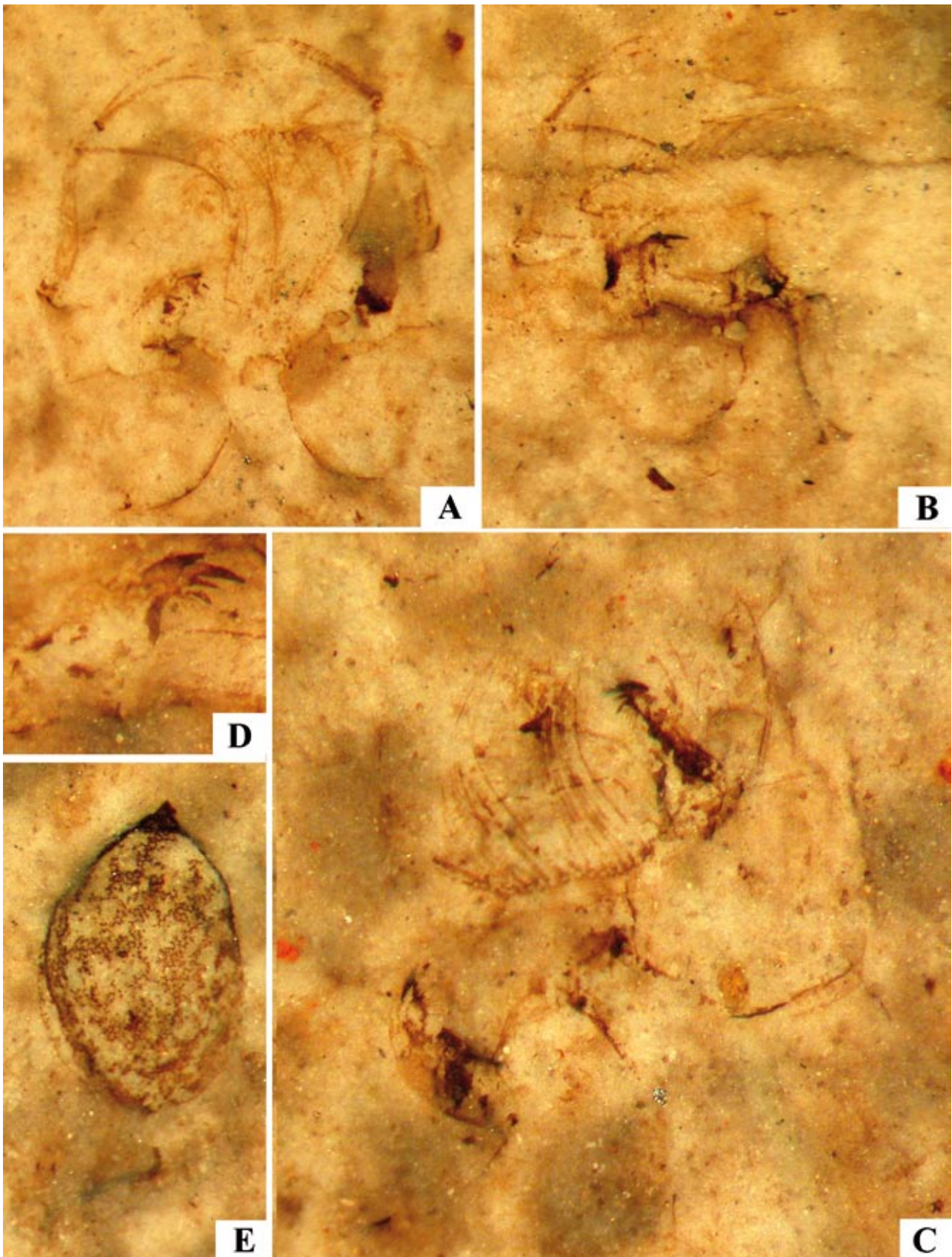


Figure 1. *Hypsocorethra toficola* Kalugina, 1985 (Uda, J₃ of Transbaikalia). A–D. Heads of larvae: A – PIN 3053/1273a; B – PIN 3053/711a; C – PIN 3053/1512a; D –PIN 3053/1276a, mandible. E. Thoracic horn of pupa PIN 3053/1274.

In *Hypsocorethra* the labral filaments likewise vary in number from 12 to 15 pairs and are probably comparable with those in *Cryophila*, placed in one row, without differentiated median pair and not divided into a pair of brushes; the antennae are typically prehensile, and the mandibles are predatory with large chitinized teeth distinguishing them from Culicidae.

The anal fan in *Hypsocorethra* consists of palmate setae. The larvae of *H. toficola* are usually preserved as exuvia or isolated head capsules, so the specimen with unclear “siphon shadows” (PIN 3053/868, mentioned in Lukashevich 1996b) can not be a proof of siphon presence and state of its development, as well as the absence of visible air sacs does not mean their real absence. So the struc-

ture of hydrostatic and tracheal systems remains unclear (in *Eucorethra* due to connection with water surface the siphon is strongly developed, and air sacs in the thorax and abdomen are absent). As a result, the hypothesis that *Hypsocorethra* was a surface predator similar to *Eucorethra* remains doubtful.

Mesocorethra levis Kalugina, 1993 (Sheviya, J₃/K₁ of Transbaikalia – Fig. 3) can be compared with a larva of another modern genus, *Promochlonyx* Edwards, 1930, both having apparently functional siphon. The larvae are quite rare and not perfectly preserved. The head capsule is broad, moderately elongated. Labral filaments (not mentioned in original description) are not numerous, their number is likely to be similar to those in *Promochlonyx* (no more than

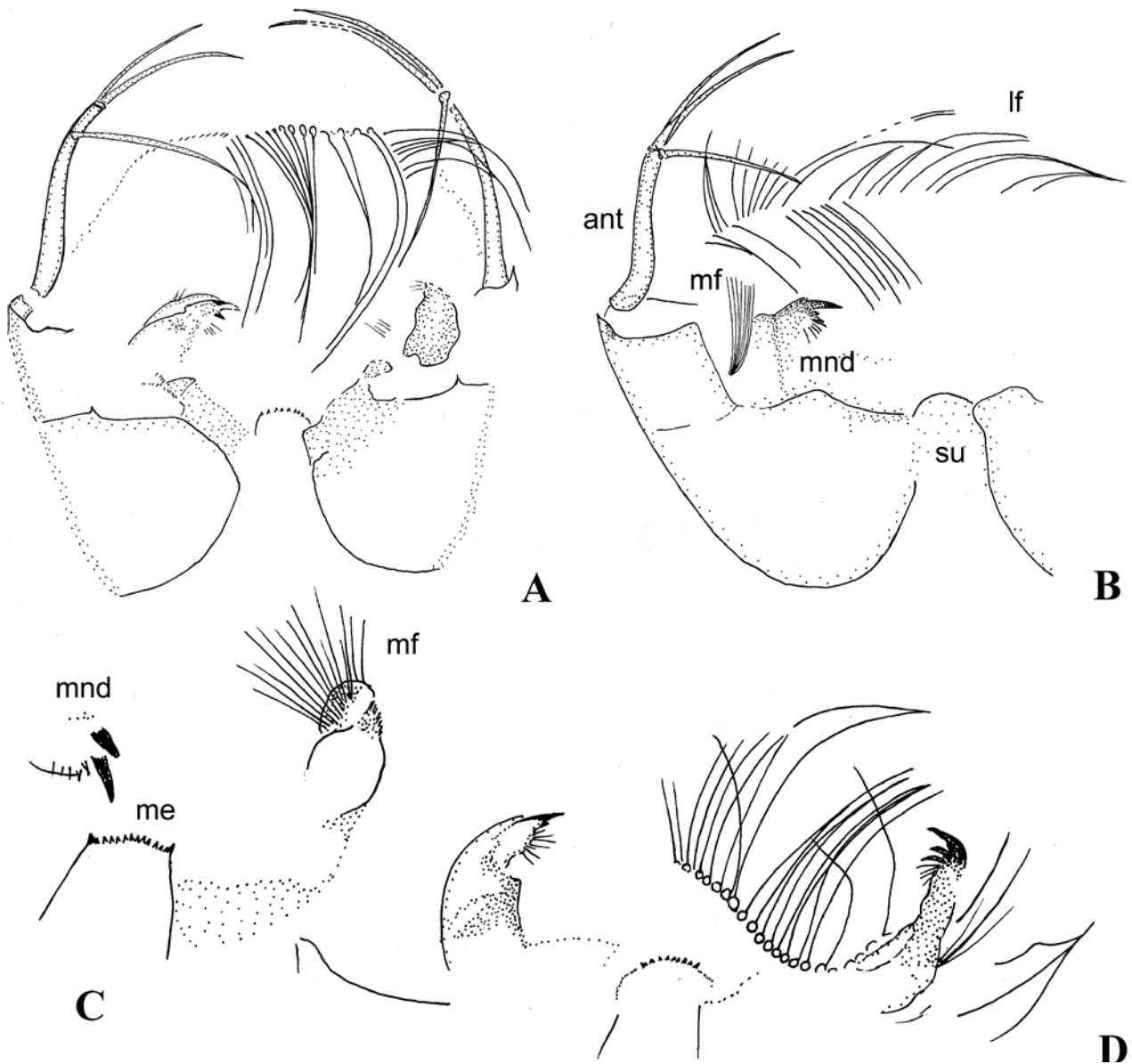


Figure 2. Heads of larvae of *Hypsocorethra toficola* Kalugina, 1985 (Uda, J₃ of Transbaikalia). A – PIN 3053/1273a; B – PIN 3053/711a; C – PIN 3053/1518a; D – PIN 3053/1512a. Abbreviations: ant – antenna, me – mentum, mf – mandibular fan, mnd – mandible, lf – labral filaments, su – submentum.

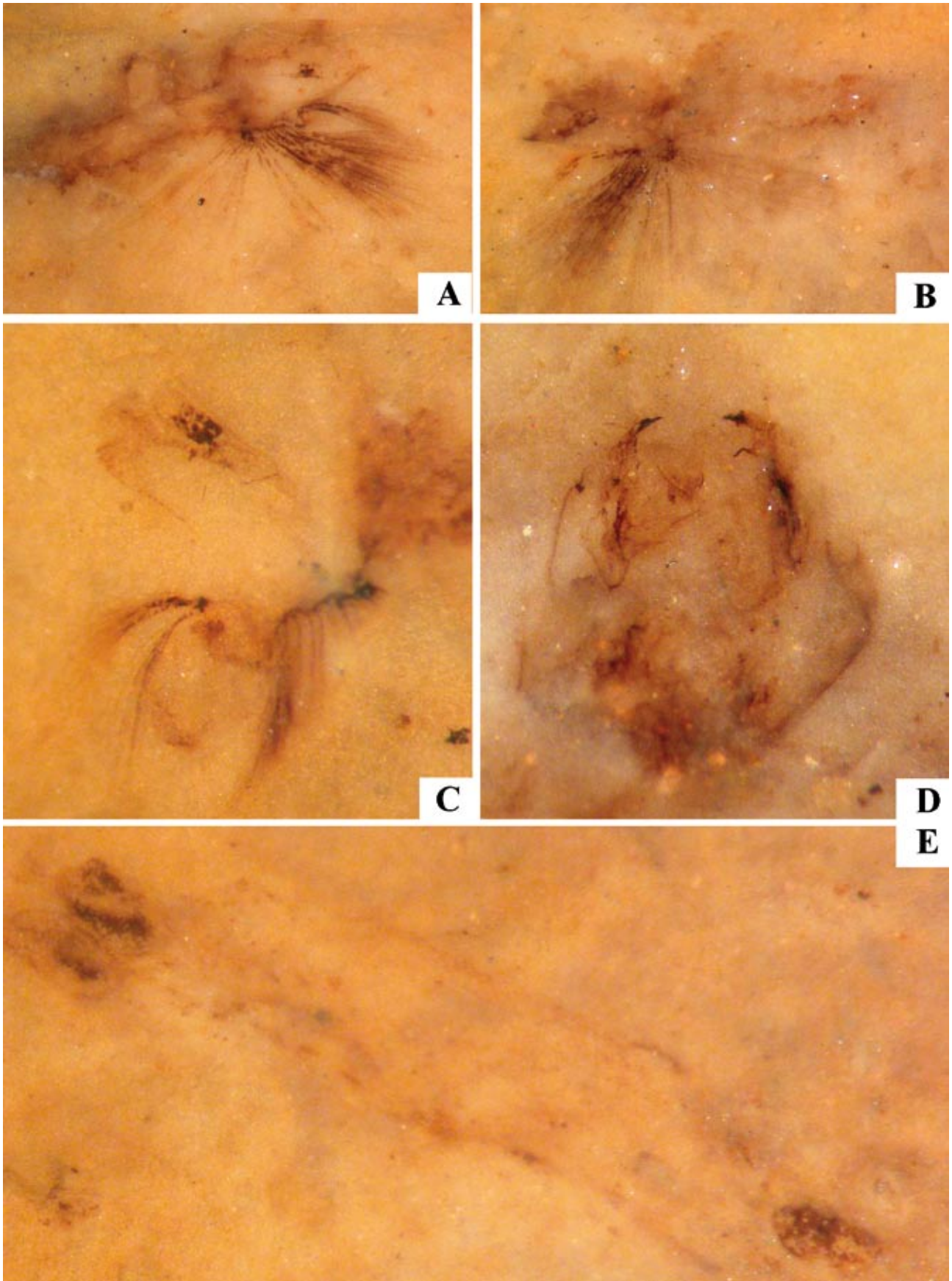


Figure 3. Larvae of *Mesocorethra levis* Kalugina, 1993 (Sheviya, J₃K₁ of Transbaikalia). A, B – PIN 3795/1272, anal segments with siphon, positive and negative impressions; C – PIN 3795/1282, anal segments with siphon; D – PIN 3795/469, head; E – PIN 3795/1058, presumable larval body with two pairs of air sacs.

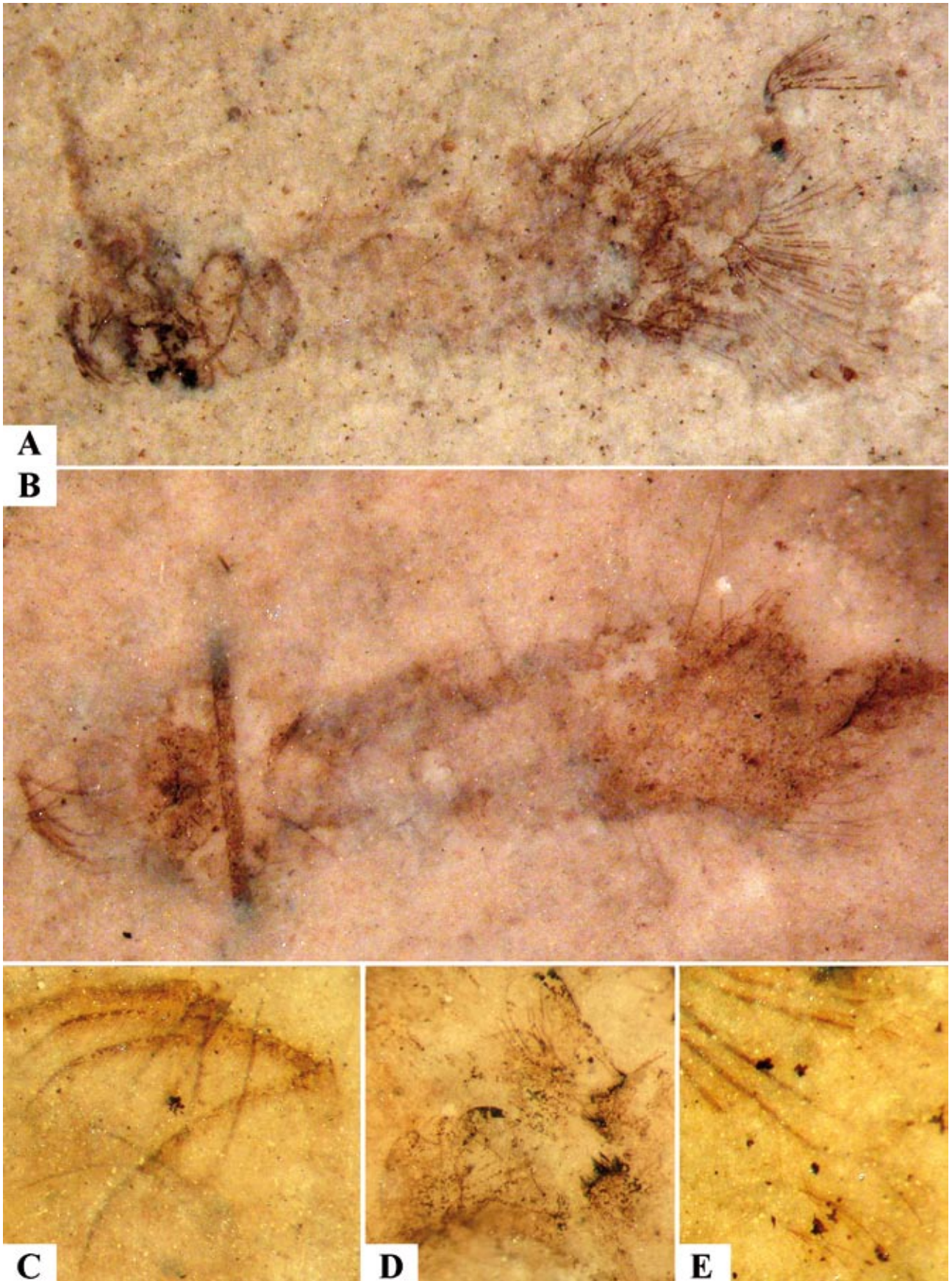


Figure 4. Larvae of *Chironomaptera scobloi* Kalugina, 1985 (Mogzon, J₃ of Transbaikalia). A, E - Paratype PIN 3084/46a: A – total view, E – plumose setae of anal fan; B, C – PIN 3084/230: B – total view, C- antennae and labral filaments; D – PIN 3084/233, two mandibles with mandibular fans, maxilla and mentum with apical teeth.

4 pairs – Colless 1986). The siphon, bearing large lobes, is slightly longer than broad (Kalugina 1993: fig. 2b). On Fig. 3B one can see the pointed tip of siphon, similar to that described and figured in *Chironomaptera collessi* Jell et Duncan, 1986 (Koonwarra, K₁ of Australia; Jell & Duncan 1986: figs. 53D–F). However, on the positive impression of same specimen and on impression of another specimen (Fig. 3A, C) it becomes obvious that the siphon is not pointed (and so is not similar to extant culicid *Mansonia* Blanchard, 1901), but has a set of lobes. So it is probably similar to the siphon of *Eucoethra*, as noticed by Kalugina. The anal fan consists of palmate setae, and pigmented air sacs are apparently present in the thorax and abdomen and one pair is larger (usually, thoracic one, but any ends of body are not preserved – Fig. 3E). When the genus was described, Kalugina wrote (1993: 122) that among described Mesozoic chaoborids it is the most probable ancestor of Culicidae (due to elongate proboscis in females and apparently functional larval siphon).

Mesozoic chaoborid larvae were very diverse not only due to the character combinations unknown in extant genera. Several features unknown in living chaoborids were discovered in the Mesozoic ones, first of all, simple setae on the larval body – one of characters used as diagnostic for Chironomapterinae and revealed in *P. tugnicus*, *H. toficola* and *Chironomaptera scobloi* (Kalugina & Kovalev

1985). In modern Chaoboridae usually all setae are simple only in the first instar larvae (Monchadsky 1936).

Chironomaptera scobloi Kalugina, 1985 (Mogzon, J₃ of Transbaikalia – Figs 4, 5) possess two more peculiarities: dense body pubescence (Kalugina & Kovalev 1985: fig. 30) and secondary setulae on apical setae of antennae. The absence of such body pubescence in modern Culicoidea is considered an adaptation of active planktonic predators which must move with their head forward (Monchadsky 1936, 1939). Similar heavy pubescence, normal for living culicids and exceptional among living chaoborids, is found in the larvae of *Eucoethra* that have no need to move forwards rapidly being surface predators. Another peculiarity of *Ch. scobloi* – numerous secondary setulae on the three apical setae of prehensile antennae – is found in Culicoidea for the first time. Surely, such microscopical fringes of setulae are more reasonable in the filter apparatus, but three apical setae are not enough for filtering. On antennae of Culicidae pubescent setae also occur, but they are not the apical setae, but constitute a special antennal tuft more proximally, with relative length and number of plumose setae in the tuft varying: the tuft is best developed in typical filter feeders, helping to direct the water current during filtration (Maslov 1967). Probably, pubescent apical setae of antennae in *Ch. scobloi* constitute a step in the same direction, but on a different morphological base.

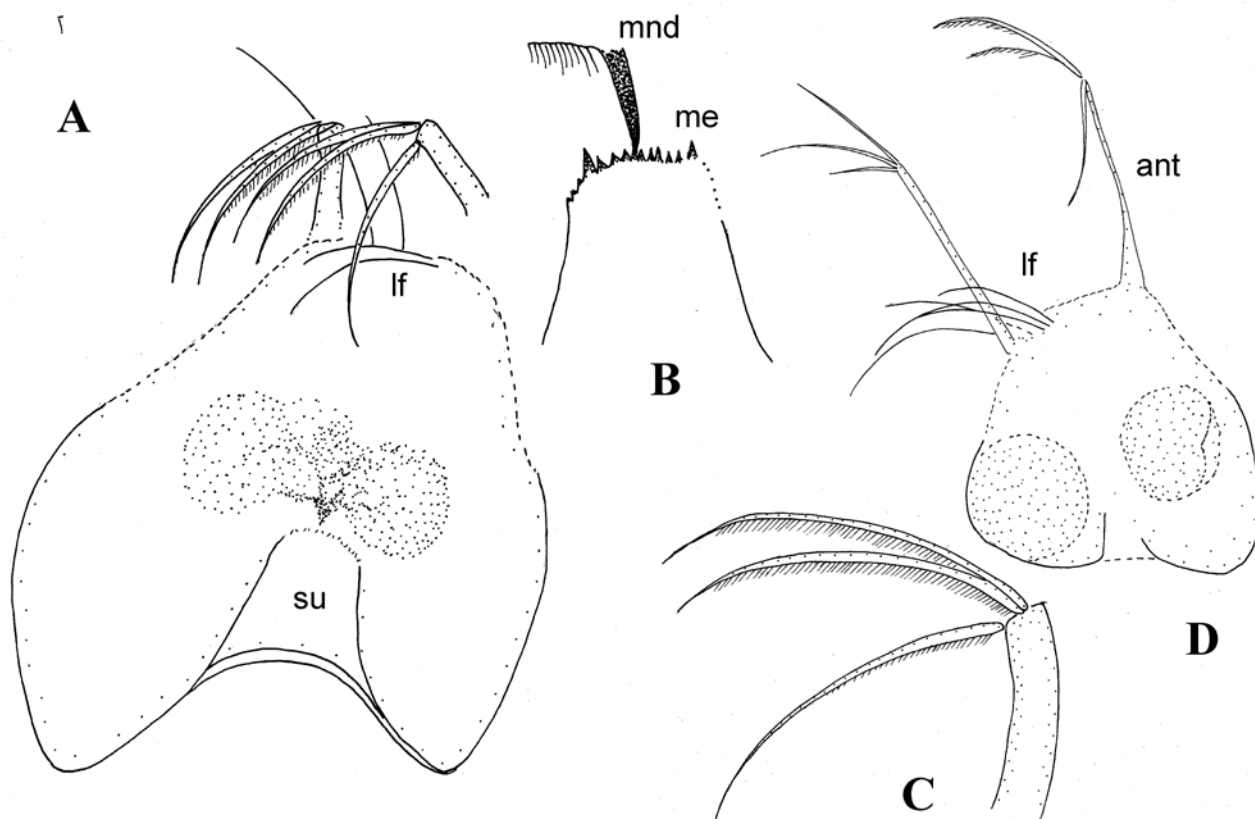


Figure 5. Heads of larvae of *Chironomaptera scobloi* Kalugina, 1985 (Mogzon, J₃ of Transbaikalia). A–C – PIN 3084/230: A – head, B – mandible and mentum, C – antenna; D – PIN 3084/215. Abbreviations: ant – antenna, me – mentum, mnd – mandible, lf – labral filaments, su – submentum.

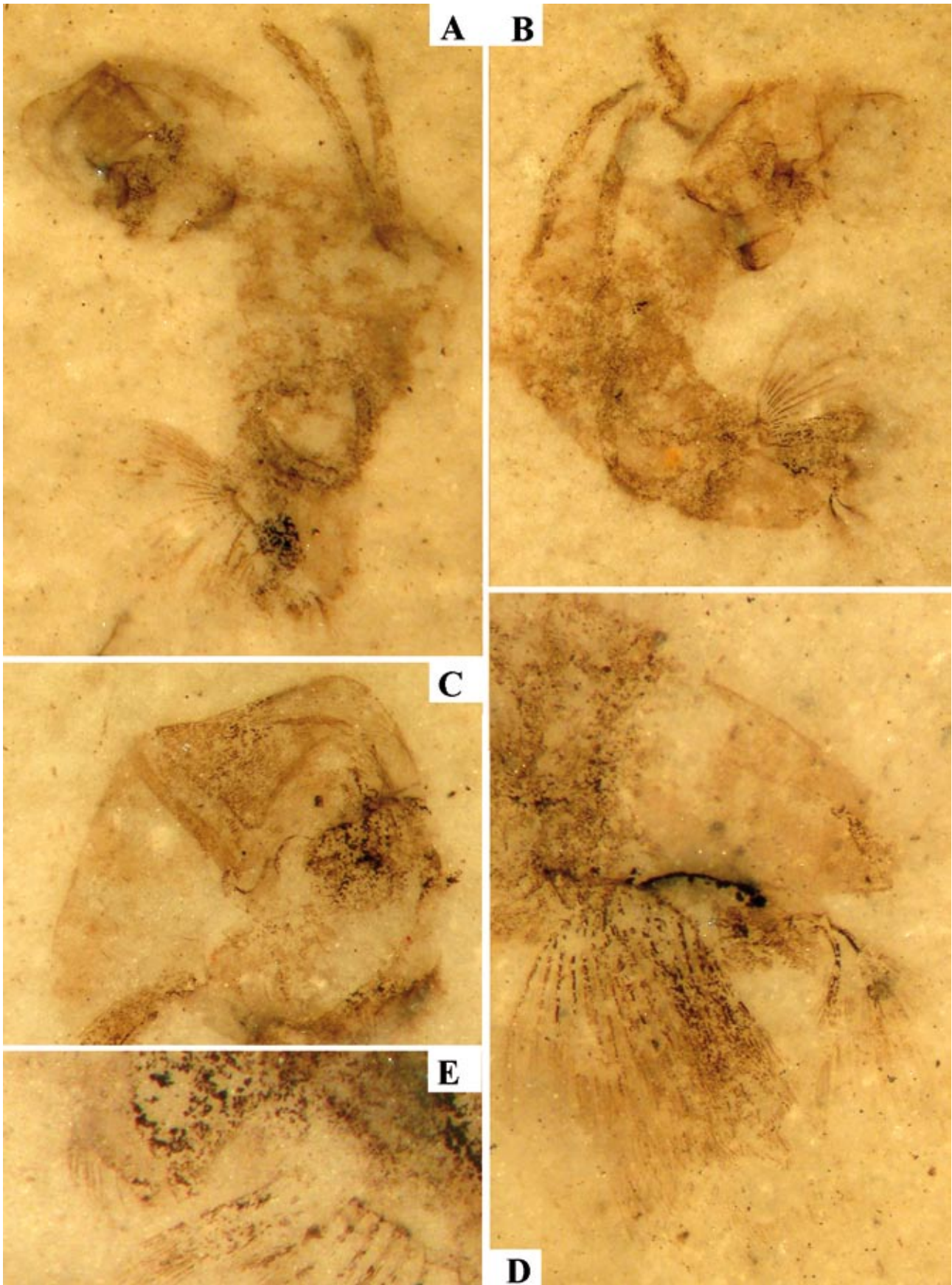


Figure 6. Larvae of Chaoboridae gen. sp. (Mogzon, J₃ of Transbaikalia). A - PIN 3084/223, total view; B - PIN 3084/222, total view; C, D - PIN 3084/221: C - head; D - anal segments with siphon and palmate setae of anal fan; E - PIN 3084/248, presumable anal apparatus and distal part of anal fan base.

So the mode of life of *Ch. scobloi* with such character set remains unclear. The moderately elongated head with antennal separation subequal to length of shaft, well developed submentum and mentum with apical teeth, mandibles with large sclerotized teeth and mandibular fan, and possibly reduced siphon are similar to *Cryophila*. Not very numerous labral filaments (not mentioned in original description), plumose setae of anal fan, and apparent absence of air sacs distinguish the extinct genus from the extant one. However, the absence of visible air sacs on impressions do not mean they were indeed absent, because in the case of unpigmented air sacs it is sometimes impossible to trace them even on microscope slides (as in *Cryophila* and *Mochlonyx* – pers. obs.). One can suppose that pubescence of the body and antennae indicate a passive catcher of very small objects rather than an active predator, as hypothesized for culicid ancestors by Kalugina (1977).

Among unique peculiarities of Mesozoic chaoborids the most interesting in respect of culicid origin is the larva possessing mouthparts presumably adapted for filter-feeding. As mentioned above, numerous labral filaments of Culicidae are divided into two lateral brushes (lobes, tufts, flabellae of authors) and median lobe that are not identical in terms of the feeding mechanism. As shown by Wesenberg-Lund and detailed by Maslov (1967) for species of *Culiseta* Felt, 1904 (one of the most generalized genera of the family), typical filter feeders have brushes set far apart of each other and separated by the broad median lobe; each brush is fairly sharply subdivided into inner and outer portions, the latter turned sideways. Typical periphytophages have noticeably narrower median lobe and lateral brushes not so widely set apart with the outer filaments arching inwards and inner ones thicker, with a typical S-shape bend and usually with tiny denticles; the separation of each lateral brush into two tufts is not distinct. The labrum of *C. (Allotheobaldia) longiareolata* (Macquart, 1838), periphytophage with facultative predation, has specific features of this second type without any specialized adaptations of other predatory culicid larvae.

The only modern chaoborid filter-feeder, *Australomochlonyx*, is evidently aberrant, without numerous labral filaments but with very small antennae and enormous complex mandibles modified for filter feeding: hypertrophied, bearing a conspicuous fan of more than hundred of long microscopically fringed hairs with apical group of 3 blades (Colless 1986).

Chaoboridae gen. sp. (Mogzon, J₃ of Transbaikalia, same locality and sometimes same rock slabs as *Ch. scobloi*; yet undescribed - Figs 6–8) show the head dissimilar to *Australomochlonyx*, but looking like a more gracile version of *H. toficola*: well-developed antenna thinner with apical setae shorter than half length of shaft, and labral filaments very numerous (about 100), quite suitable for filter-feeding, probably placed in several (?3) rows (if dark spots on the labrum are the bases of filaments – Fig. 7A) and divided into two brushes, as in Culicidae, but not set far apart of each other. The description of a new species will

be made later, based on all stages of development (there are some problems due to the presence of *Ch. scobloi* in the same locality). On the well-preserved impressions one can see many important features:

- larval body not pubescent, not transparent;
- head not elongated;
- antennal separation greater than length of shaft;
- thin antenna with apical setae shorter than half length of shaft, without antennal tuft;
- labral filaments numerous (about 100) and long (comparable to height of head and antennal length), probably placed in several (?3) rows and divided into two brushes, in which straight inner filaments possibly slightly thicker;
- submentum large;
- two pairs of elongate air sac with larger thoracic pair;
- well developed siphon not long and without any setae and sclerotization;
- palmate setae of anal fan.

So, terminal segments of larval abdomen are similar to those of *Australomochlonyx* (Colless 1986: fig. 51), and probably even an everted anal apparatus on ninth abdominal segment can be observed in one impression (Fig. 6E). This apparatus is known in all chaoborids (even in filter-feeders) and Corethrellidae, and nowhere else (Edwards 1932). It is one of specific adaptations for a peculiar mode of predation: chitinous remains of prey are removed by crop eversion, and anal apparatus helps to clean the everted crop and to cut the peritrophic membrane (Monchadsky 1939, 1945).

So far as the presence of anal apparatus is still doubtful, among other features the most important is the presence of two pairs of air sacs. They look not like normal chaoborid sacs but are narrow and elongate, more similar to tubes, the quite long second pair is possibly not restricted to the seventh abdominal segment (on microscope slides of extant *Mochlonyx* the length of this pair is sometimes much longer than the segment length – pers. obs.). Very similar tubes – slightly dilated portions of tracheal trunks – were described in the thorax and abdomen of *Chironomaptera collessi* (Jell, Duncan 1986: fig. 52) and in the thorax of several *Culiseta* species (Monchadsky 1936). However, Culicidae possess only one pair of air sacs, if any! From any point of view two pairs of larval air sacs are an apomorphy of at least some part of Chaoboridae (unknown in any other family), so the discussed larvae should belong to the family.

To our mind, all the characters and finds discussed above confirm the opinion of Kalugina (1977): Culicidae are a derivate of Chaoboridae, and among diverse chaoborids that flourished in the Jurassic, presumably some forms ancestral to Culicidae existed, with little specialized larva of the catcher type (not obviously predatory) or filter feeders. Further investigations based on all stages of development are necessary.

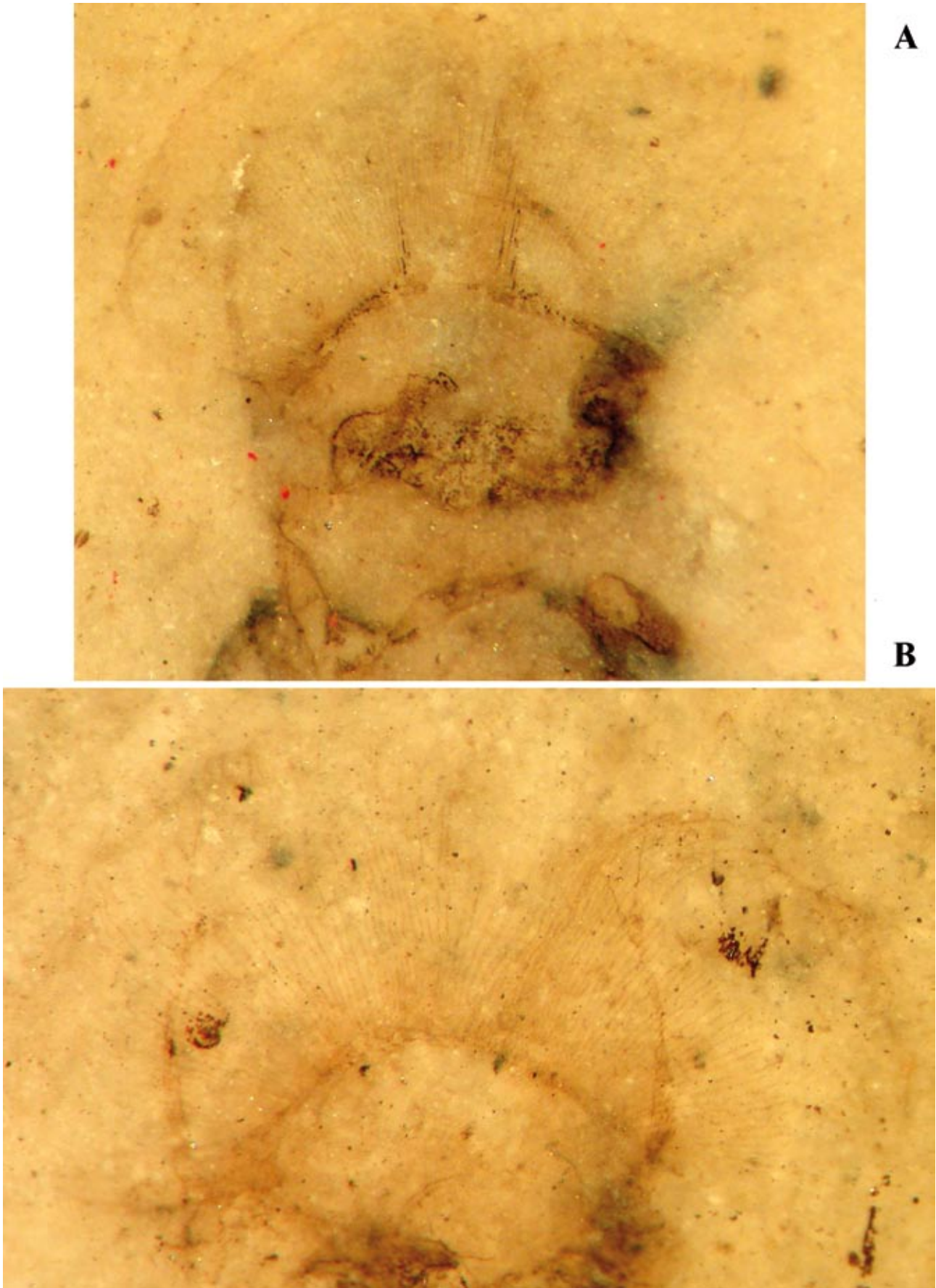


Figure 7. Larvae of Chaoboridae gen. sp. (Mogzon, J₃ of Transbaikalia). A – PIN 3084/226, head; B – PIN 3084/225, antennae and labrum with labral filaments.

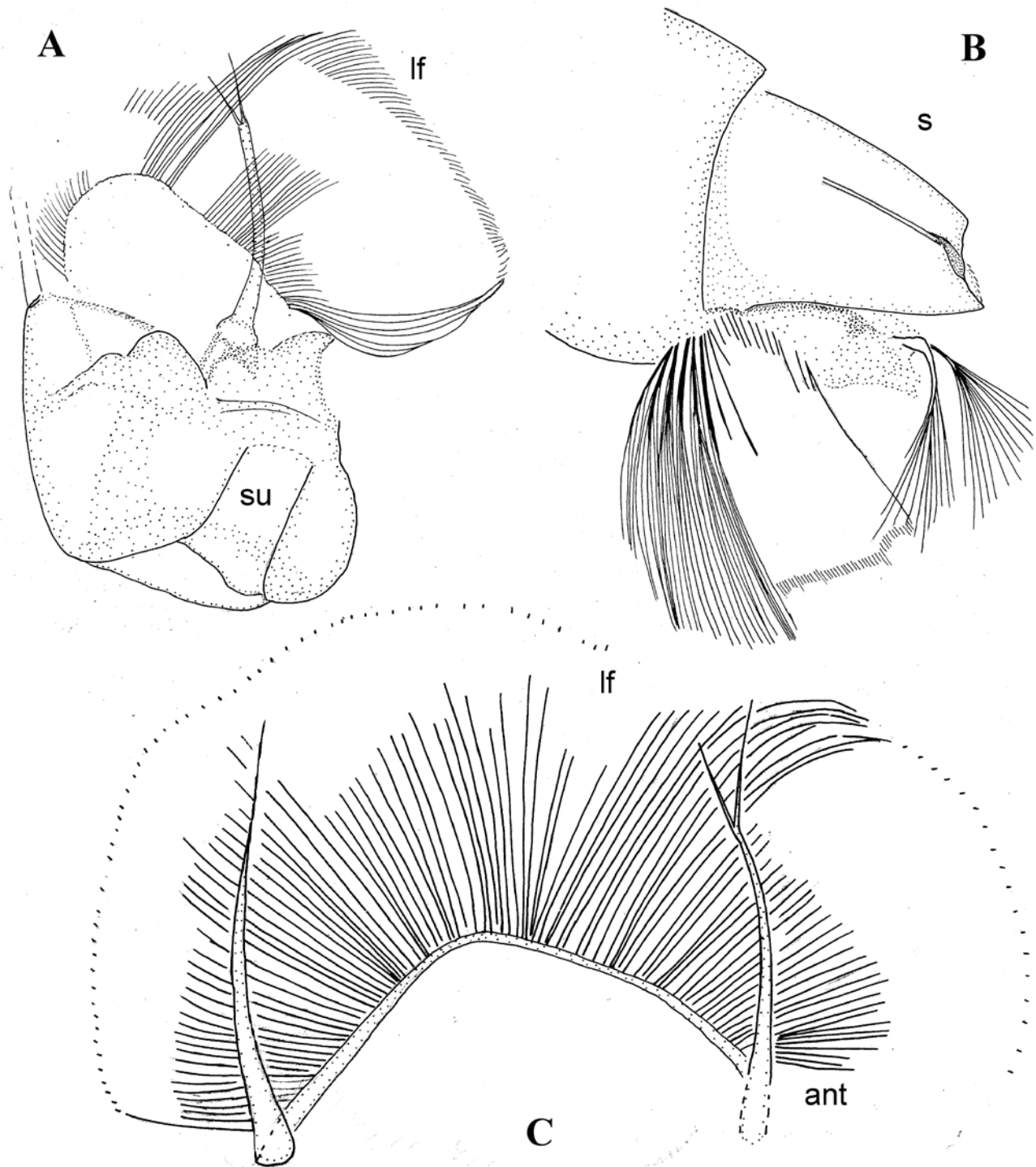


Figure 8. Larvae of Chaoboridae gen. sp. (Mogzon, J₃ of Transbaikalia). A – PIN 3084/222, head; B – PIN 3084/221, anal segments with siphon and palmate setae of anal fan; C – PIN 3084/225, fan of labral filaments and antennae. Abbreviations: ant – antenna, lf – labral filaments, s – siphon, su – submentum.

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