

New data on taxonomy and evolution of fossil and Recent Prophalangopsidae (Orthoptera: Hagloidea)

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Abstract. The family Prophalangopsidae is ancestral for two large Recent superfamilies: Tettigonioidea and Stenopelmatoidea. This family is known from the Early Jurassic, and it is divided into 5 fossil (including one new) and one Recent subfamilies. The partial revision of their generic composition shows that this family was most numerous and diverse in the Early Cretaceous of temperate zone of Old World, but this information is only preliminary. The mode of life of fossil Prophalangopsidae (Recent forms are practically not studied) was more or less similar to that of some Recent Stenopelmatoidea and Tettigonioidea, but with important distinctions connected with somewhat different type of function of the tegminal stridulatory apparatus. The main possible trends in evolution of this apparatus are (1) the displacement of stridulatory areas at the base of tegmina accompanied by their partial reduction and the improvement of cryptic appearance of male during stridulation, and (2) the significant increase of these areas accompanied by deterioration of male cryptic appearance during stridulation. The origin of Stenopelmatoidea and Tettigonioidea from Prophalangopsidae is a possible result of analogous processes.

Key words: Orthoptera, Prophalangopsidae, taxonomy, paleontology, evolution

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I. CHARACTERISTICS OF THE FAMILY

Prophalangopsidae is the youngest family of the superfamily Hagloidea (a primitive superfamily of Ensifera with tegminal stridulatory apparatus in male known from Triassic to now). This family is ancestral for two large Recent superfamilies: Tettigonioidea and Stenopelmatoidea. The origin of Prophalangopsidae from the Triassic-Early Cretaceous family Haglidae is possibly connected with distinct improvement of flying function of hind wings and with decrease of importance of stridulatory apparatus (GOROCHOV 1995).

The improvement of hind wings consists of widening of their anal part and of appearance of rather long additional (secondary) longitudinal vein obliquely connecting MP+CuA1 with CuA2 (for comparison see Figs 2: Haglidae and 5: Prophalangopsidae). The widened hind wings of Prophalangopsidae need a larger space under tegmina during the rest position.

The tegmina raise themselves a little in this position, and the characteristic fold appears between the proximal part of their costal area (contacting the body) and other parts of tegmina (embracing hind wings). Along this fold, the new longitudinal vein from transverse veinlets between branches of Sc (false C) appears (see Figs 1: Haglidae and 3, 4: Prophalangopsidae). These characters of hind wing and tegmina are most important for distinguishing the Prophalangopsidae and their descendants from other Hagloidea (but secondary reduction of tegminal false C is rather common also as a result of wing shortening or change of position of hind wings under tegmina).

There are two opposite trends in evolution of stridulatory apparatus of Hagloidea and their descendants: improvement and reduction. The display of these trends in Prophalangopsidae is somewhat different than in more primitive Hagloidea and Grylloidea. One of most common ways of improvement of stridulatory apparatus in the latter groups is a widening of stridulatory areas in the middle part of tegmina (up to occupation of most part of tegmina) (Figs 6-8). This way causes diminishing the cryptic appearance of male during stridulation, as the distal parts of tegmina have a big amplitude of movement. The appearance of new predatory vertebrates with good visual analyser in the middle of Mesozoic may have caused searching the new ways of improvement of stridulatory apparatus. One of these ways was the reduction of stridulatory areas in the middle part of tegmina and the development of analogous areas in only proximal part of tegmina. This way allows to diminish the amplitude of movement of tegminal apici during stridulation. The maximal perfection of this type of stridulation was reached by Tettigonioidea. Other descendants of Prophalangopsidae – the Stenopelmatoidea lost ability to tegminal stridulation. Prophalangopsidae are an intermediate group between Tettigonioidea, Stenopelmatoidea, and more primitive Hagloidea, therefore the above-mentioned trends are very important for their evolution (and consequently for their taxonomy).

The structure of the body of Prophalangopsidae is also intermediate between Tettigonioidea and Stenopelmatoidea (Figs 11, 25, 26): their head is rather high and round in profile (without rostral tubercles characteristic of majority of Tettigonioidea and some Stenopelmatoidea), their pronotum has a distinct (sometimes rather large) hind lobe, their legs are with numerous spines and spurs, open tympana on both sides of fore tibiae, hind femora adapted to jumping, and tarsi provided with four narrow segments (sometimes two proximal segments are more or less fused with each other), their male tegmina are with stridulatory apparatus (females do not have this apparatus), their male abdominal apex bears simple, short cerci, diverse copulatory processes and hooks on paraprocts and sometimes on tergites, well developed genital plate provided with rather small styli, and membranous (hagloid type) genitalia (in Recent representatives), their ovipositor is well developed and rather long (in fossil forms) or probably partially reduced and with rather long styli on apices of rudimentary upper valvae (in one Recent species).

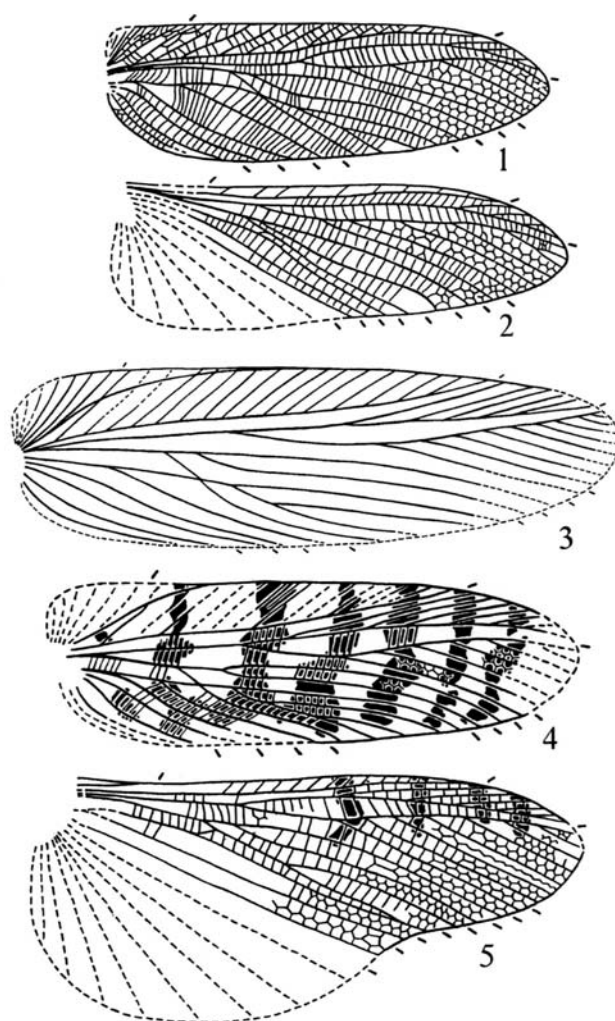
The mode of life of fossil representatives of this family was possibly more or less similar to some Recent Stenopelmatoidea and Tettigonioidea. They may had phyto-geophilous adaptations: many of them had striped coloration somewhat imitating small branches or leaves of Mesozoic plants, some of them fed on *Classopollis* pollen (phytophagous or polyphagous habits) (KRASSILOV et al. 1997), sometimes the apical spurs of hind tibiae were rather short (characteristics of phytophilous forms), but their tarsi were without arolium and strongly widened pulvillae on sole (geophilous adaptations), and they probably laid eggs into soil. Some of fossil Prophalangopsidae were provided with rather strong spines on fore and middle tibiae; they may have been predators. The mode of life of Recent Prophalangopsidae is practically not studied, but they are probably geophilous insects, as their tarsal segments are more or less distinctly fused, and apical spurs of hind tibiae are comparatively long (Figs 25, 26) (both characters are characteristic features of geophilous forms). I cannot exclude that one Recent genus (*Tarragoilus* GOROCHOV, 2001) has ability of digging primitive burrows (reduction of ovipositor suggests this mode of life).

II. CHARACTERISTICS OF SUBFAMILIES

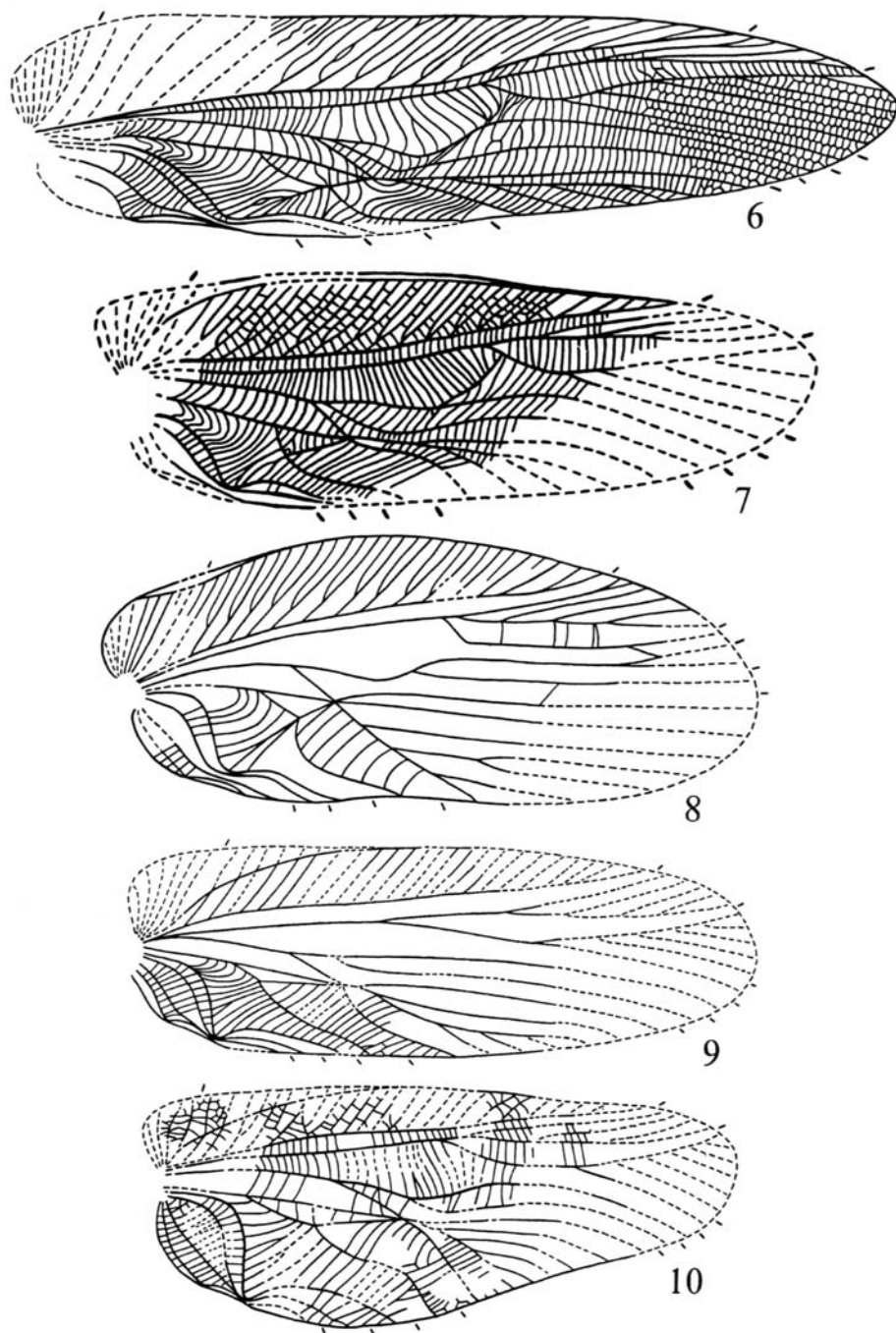
Prophalangopsidae consists of five fossil and one Recent subfamilies:

1. **Protaboilinae** (*Protaboilus* GOROCHOV, 1988, Lower Jurassic, Middle Asia – Figs 3, 9).

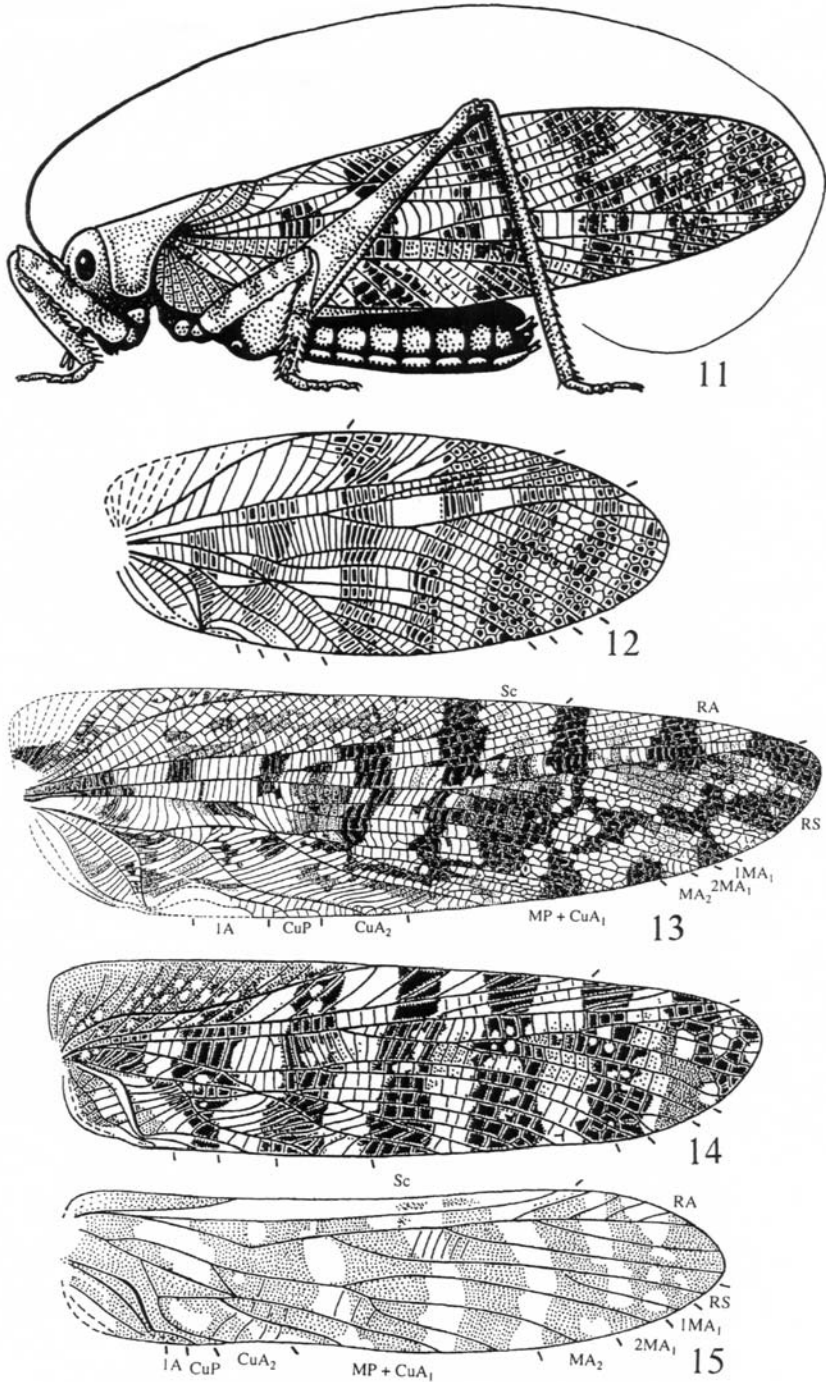
2. **Aboilinae** (*Sunoprothalangopsis* HONG, 1982, Middle Jurassic, China; *Bacharaboilus* GOROCHOV, 1988, Middle Jurassic, Mongolia, – Fig. 10; *Aboilus* MARTYNOV, 1935, Upper Jurassic, Kazakhstan and Siberia – Figs 4, 5, 11-14; *Apsataboilus* GOROCHOV, 1990, Upper Jurassic or Lower Cretaceous, Siberia; *Prophalangopseides* SHAROV, 1968 – Fig. 17 and *Tettaboilus* GOROCHOV, 1988 – Fig. 18, Lower Cretaceous, Siberia; *Utanaboilus* GOROCHOV, 1990, Lower and possibly Upper Cretaceous, Siberia – Fig. 16; possibly *Brunneus* HONG, 1983 from Middle Jurassic of China; *Pseudohagla* SHAROV, 1962 from Middle-Upper Jurassic of Siberia; *Pycnophlebia*



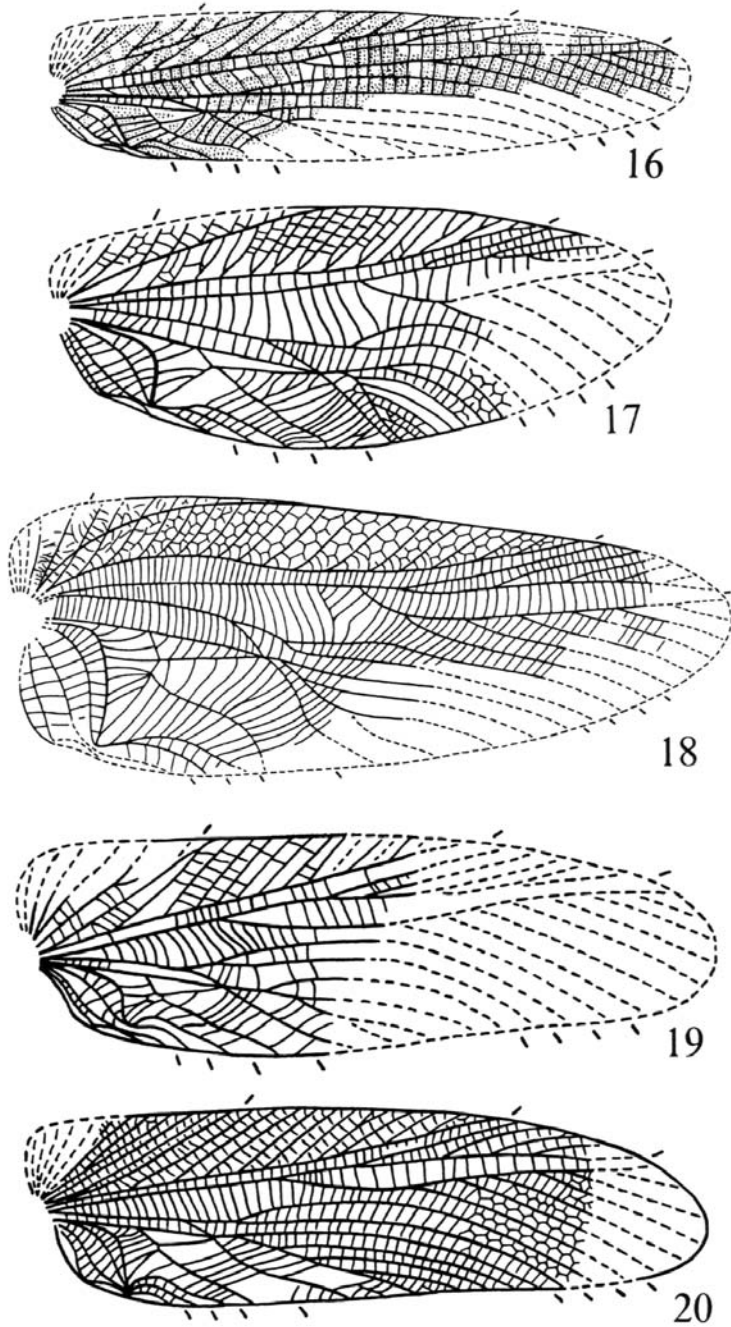
Figs 1-5. Haglidae (1, 2) and Prophalangopsidae (3-5). 1, 2: female tegmen and hind wing of *Prohagla superba* RIEK (Triassic, Australia); 3: female tegmen of *Protaboilus* sp. (Lower Jurassic, Middle Asia); 4, 5: female tegmen of *Aboilus* sp. and hind wing of *A. maculatus* (MARTYNOV 1935) (Upper Jurassic, Middle Asia).



Figs 6-10. Haglidae (6-8) and Prophalangopsidae (9, 10), male tegmen; 6. *Voliopus ancestralis* GOROCHOV (Triassic, Middle Asia); 7. *Archaboilus shurabicus* MARTYNOV (Lower Jurassic, Middle Asia); 8. *Bacharia zherichimi* GOROCHOV (Middle Jurassic, Mongolia); 9. *Protaboilus praedictus* GOROCHOV 1988 (Lower Jurassic, Middle Asia); 10. *Bacharaboilus mongolicus* GOROCHOV 1988 (Middle Jurassic, Mongolia).



Figs 11-15. Aboilinae, male (Upper Jurassic, Kazakhstan). 11. reconstruction of *Aboilus aulietus* SHAROV; 12. tegmen of *A. columnatus* MARTYNOV 1935; 13. tegmen of *A.? femineus* GOROCHOV; 14. tegmen of *A.? zebra* GOROCHOV; 15. tegmen of *Karatailus micropterus* GOROCHOV 1996.



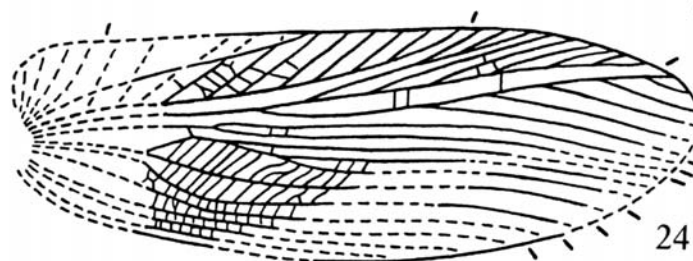
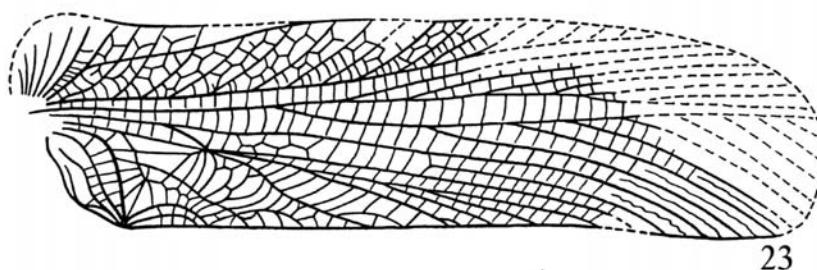
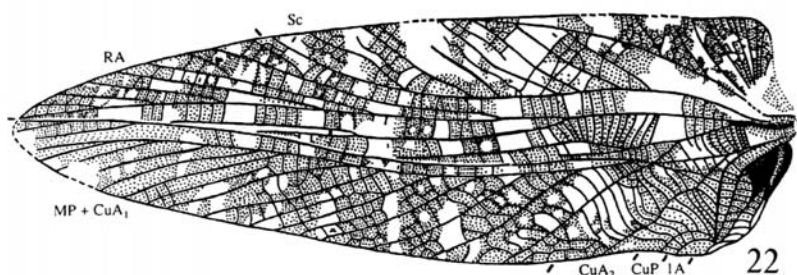
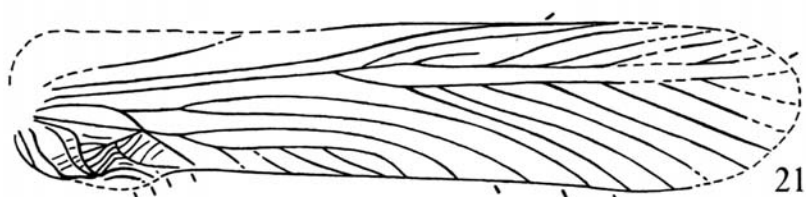
Figs 16-20. Aboilinae (16-18) and Chifengiinae (19, 20), male tegmen: 16. *Utanaboilus pulchellus* GOROCHOV 1990 (Lower/Upper Cretaceous, Siberia); 17. *Prophalangopseides vitimicus* SHAROV 1968 (Lower Cretaceous, Siberia); 18. *Tettaboilus pulcher* GOROCHOV 1988 (Lower Cretaceous, Siberia); 19. *Ashanga clara* ZHERIKHIN 1985 (Middle/Upper Jurassic, Siberia); 20. *Parahagla sibirica* SHAROV 1968 (Lower Cretaceous, Siberia).

DEICHMULLER, 1886 from Upper Jurassic of Germany; *Nipponohagla* FUJIANA, 1978 from Lower Cretaceous of Japan; *Baissaboilus* GOROCHOV, 1996 from Lower Cretaceous of Siberia, and enigmatic *Karatailus* Gorochov, 1996 from Upper Jurassic of Kazakhstan – Fig. 15).

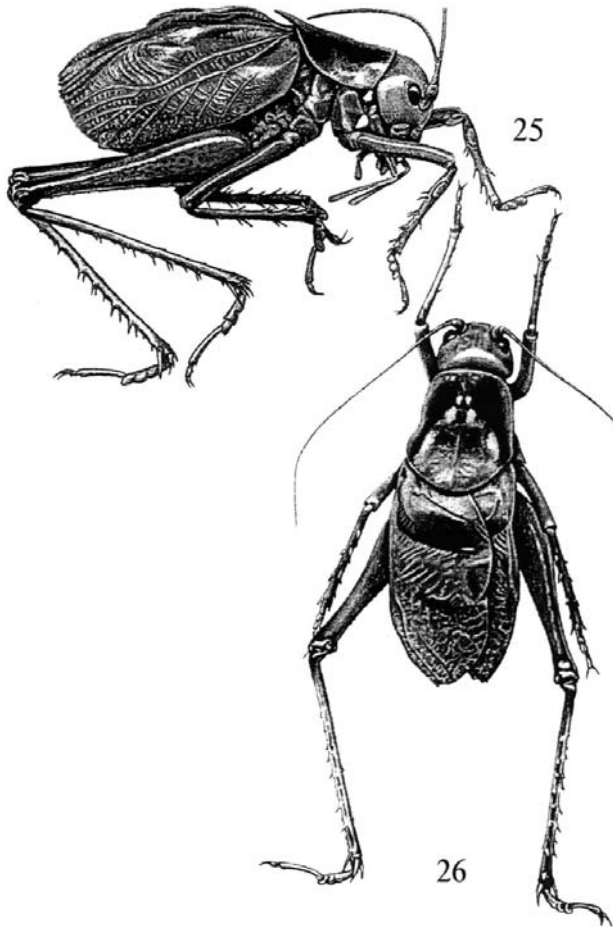
3. **Chifengiinae** (*Ashanga* ZHERIKHIN, 1985, Middle or Upper Jurassic, Siberia – Fig. 19; *Parahagla* SHAROV, 1968, Lower Cretaceous, Siberia – Fig. 20; *Chifengia* HONG, 1982; *Hebeihagla* HONG, 1982 and *Habrohagla* REN, LU, GUO & JI, 1995, Lower Cretaceous, China).

4. **Termitidiinae** (*Termitidium* WESTWOOD, 1854, Lower Cretaceous, England – Fig. 21).

5. **Tettohaglinae** subfam. n.



Figs 21-24. Prophalangopsidae (21, 22), Haglotettigoniidae (23), and possible Anostostomatidae (24), tegmen: 21. *Termitidium ignotum* WESTWOOD 1854, male (Lower Cretaceous, England); 22. *Tettohagla problematica* GOROCHOV, male (Lower Cretaceous, Siberia); 23. *Haglotettigonia egregia* GOROCHOV, male (Lower Cretaceous, Siberia); 24. *Zeuneroptera scotica* (ZEUNER) (Paleocene, Scotland).



Figs 25, 26. Male of *Tarragoilus diuturnus* GOROCHOV 2001 (China, Sichuan; Recent) in lateral (25) and apical view (26).

6. Recent **Prophalangopsinae** (*Prophalangopsis* WALKER, 1871, former British India – Figs 29, 30; *Tarragoilus* GOROCHOV, 2001 – Figs 25-28 and *Aboilomimus* GOROCHOV, 2001 – Figs 31, 32, China, Sichuan).

The systematic position of Recent Cyphoderrinae is problematic, as the venation of their tegmina is not very clear. They resemble both Hagloidea and primitive Tettigonioidea. There are also several enigmatic taxa of fossil insects which possibly belong to Prophalangopsidae, but they are insufficiently described or described from not informative fragments.

Protaboilinae are a most primitive group of this family; it is possibly ancestral for all other subfamilies. The comparison with most similar groups of Haglidae (Voliopinae, Fig. 6; Cyrtophyllitinae, Fig. 7; Bachariinae, Fig. 8) shows that a most probable sister group of Protaboilinae (and all Prophalangopsidae) are the Bachariinae. The possible general ancestor of Protaboilinae and Bachariinae had partly reduced tegminal stridulatory apparatus in the male (with narrow area in the middle part of tegmina between R and M as in *Protaboilus*, Fig. 9). Protaboilinae acquired a false C in tegmina and probably widened hind wings. Bachariinae had possibly only first elements of this process (characteristic narrow loop along costal edge of tegmina, Fig. 8), and their stridulatory area

between R and M had widened again, but proximally of the base of MA2 (Fig. 8). In all more primitive Haglidae this area was widened distally to base of MA2 (Figs 6, 7). In other Prophalangopsidae, the newly acquired widening of this area is situated near base of MA2 (Figs 10, 12-22). This difference in position of this area shows that the false C in tegmina of Cyrtophyllitinae (Fig. 7: shape of this vein is more strongly arched than in Prophalangopsidae) is only a convergence. Protaboilinae differ from all other Prophalangopsidae in the presence of arched transverse veinlets between proximal parts of CuA and CuP in male tegmina. This primitive character is very common in Haglidae, Tuphelliidae, and Hagloedischiidae.

Aboilinae are possible descendants of Protaboilinae; they constitute a most rich and diverse subfamily of Prophalangopsidae. The first Aboilinae probably had the stridulatory apparatus more reduced than in *Protaboilus* (base of CuA2 is moved to stridulatory vein, transverse veinlets between CuA and CuP are straightened). The new strengthening of this apparatus led to widening of stridulatory areas: (1) with base of CuA2 in primitive position near stridulatory vein (Middle Jurassic *Bacharaboilus* – Fig. 10; Upper Jurassic *Aboilus* – Fig. 12 and *Karatailus* – Fig. 15), (2) with base of CuA2 moved somewhat distally (Upper Jurassic *Aboilus* – Figs 13, 14; Cretaceous *Utanaboilus* – Fig. 16, *Prophalangopseides* – Fig. 17, and *Tettoaboilus* – Fig. 18). There are also the independent cases of partial reduction of this apparatus reflected in the distinct narrowing of area between R and M (Figs 13, 16). The systematic position of some imprints is in need of additional study. For instance, *Aboilus* sensu GOROCHOV includes maybe more than one genus, *Tettoaboilus distinctus* GOROCHOV, 1996 probably belongs to another genus, and an enigmatic micropterous *Karatailus* possibly does not belong to Aboilinae.

Chifengiinae are characterized by the reduction of tegminal false C. The classification of this subfamily into Prophalangopsidae is caused by remarkable similarity of its stridulatory apparatus to that of Aboilinae (Figs 19, 20). Jurassic Chifengiinae had traces of false C (Fig. 19), but Cretaceous ones lost these traces (Fig. 20). The reduction of false C may be connected with change of position of hind wings under tegmina allowing to lower the tegmina in resting position. The confirmation (or rejection) of this hypothesis will be possible when the hind wings of Chifengiinae are found. The stridulatory apparatus of Chifengiinae is partly reduced. They may be descendants of some primitive Aboilinae.

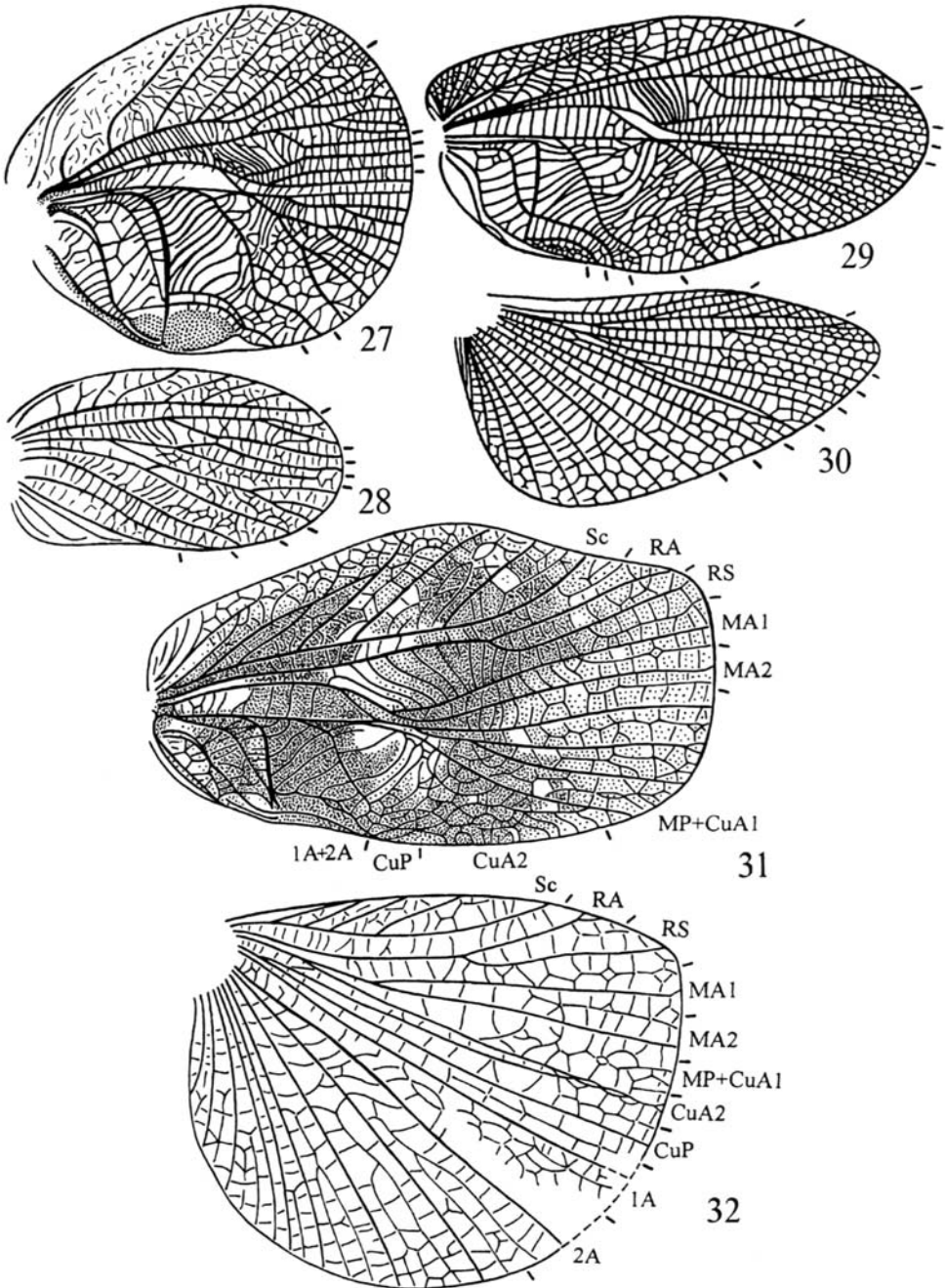
Termitidiinae had the partly reduced stridulatory apparatus also, but their tegminal false C was well developed. The study of holotype of *Termitidium ignotum* WESTWOOD 1854 and representatives of two new genera from Lower Cretaceous of England revealed that the Termitidiinae are very similar to Aboilinae and descend from them (Fig. 21).

Subfamily **Tettohaglinae** subfam. n.

D i a g n o s i s. Tegmina (Fig. 22) with well developed false C, partly reduced MA2 (with only short proximal part), and very numerous regular branches of MP+CuA1 which occupy large (long and rather wide) dorsal part of tegmina (this part reaches to tegminal apex).

C o m p o s i t i o n. *Tettohagla* GOROCHOV, 1996 (Lower Cretaceous; Siberia, Baissa).

Tettohagla was originally described as a genus of unclear systematic position (GOROCHOV 1996), as it shares some similarities with primitive Tettigonioidae (Haglotettigoniidae, Fig. 23) in the partly reduced tegminal MA2 and the small stridulatory areas of tegmina, while with the Prophalangopsidae, in the absence of mirror-like cell between CuA1 and CuA2 (this cell is present in *Haglotettigonia* GOROCHOV, 1988 – see Fig. 23, this paper). However, the partial reduction of stridulatory apparatus is usual phenomenon in Prophalangopsidae, and the partial reduction of MA2 in both groups may have independent origin, as the different rudiments of this vein are present in *Tettohagla* (proximal part, Fig. 22) and *Haglotettigonia* (distal part, Fig. 23). Aboilinae may be an ancestral group for Tettohaglinae also.



Figs 27-32. Recent Prophalangopsinae, tegmen and hind wing of male. 27, 28: *Tarragoilus diuturnus* GOROCHOV (China, Sichuan); 29, 30: *Prophalangopsis obscura* WALKER 1981 (former British India); 31, 32. *Aboilomimus sichuanensis* GOROCHOV 2001 (China, Sichuan).

The Recent possible descendants of Aboilinae (Prophalangopsinae, Tettigonioidea, Stenopelmatoidea) underwent different evolution of stridulatory apparatus. This way in Prophalangopsinae was a primitive one – the widening of stridulatory areas R-M and especially CuA1 - CuP (Figs 27, 29, 30). This group is characterized by the tendency to fusion of two proximal segments of tarsi (Figs 25, 26); main differences between three Recent genera are in structure of hind wings: primitive – Fig. 30, modified – Fig. 32, tegmen-like – Fig. 28. The way of evolution in Tettigonioidea was modified and involved the development of special stridulatory area near stridulatory vein (mirror) (Fig. 23) and the change of type of movement of tegmina during stridulation. Stenopelmatoidea lost the tegminal stridulatory apparatus (Fig. 24), but they acquired a new stridulatory apparatus – a femoro-abdominal one.

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