



The ecology, biology and larval instars of the North Caucasian population (Lake Maliy Tambukan) of *Tipula subcunctans* Alexander, 1921 (Diptera: Tipulidae)

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Abstract

Different aspects of ecology, biology and regional distribution of *Tipula subcunctans* in the North Caucasus (Lake Maliy Tambukan, 12 km south-east of Pyatigorsk) are investigated. Abundance of larvae, fecundity of females, mode of oviposition and other data are presented. First instar larvae are described and the existence of two morphological forms of fourth instar larvae is demonstrated.

Key words: North Caucasus, *Tipula subcunctans*, ecology, biology, larvae morphology

Introduction

In the scope of my studies of Tipuloidea in the North Caucasian foothills, limoniids and tipulids were collected in the basin of Bolshoy Tambukan and Maliy Tambukan (Lake Sukhoe) at salt pans situated in the forest-steppe zone in 12 km south-east of Pyatigorsk (43°57' N., 43°10' E.) at 575 m. *Tipula (Tipula) subcunctans* Alexander, 1921 (= *czizeki* de Jong, 1925), an autumn crane fly, occurs here (Lantsov 2004) including the preimaginal stages which, together with the ecology of the species, are of certain interest.

This species has been recorded as a pest in the Ukraine, Byelorussia and Germany (Maercks 1941; Sellke 1936, 1937; Savchenko 1961, 1981). It can cause a lot of harm in areas flooded during the spring-tide and winter thaws (Savchenko 1981). The fourth instar larva of *T. subcunctans* has not been thoroughly studied, unlike that of related species (Brindle 1959, 1960; Byers 1958; Theowald 1957, 1967; Savchenko 1983). Available information on the ecology is largely based on western European populations (Jong 1925; Sellke 1936, 1937; Maercks 1941; Savchenko 1961).

The works devoted to the biology and ecology of the species, as well as to other closely related *Tipula* (Sellke 1936, 1937; Maercks 1941; Hemmingsen & Theisen 1956; Theowald 1957, 1967; Brindle 1959), do not provide descriptions and drawings of the first instar larva of *T. subcunctans*. According to Pjotr Oosterbroek (personal communication) the first instar larva of this species has not been studied. Savchenko in his monograph (1983: 126) gives certain details about the first instar larva of *T. subcunctans* (referred to as *Tipula (Tipula) czizeki* de Jong, 1925), namely that the number of elongate setae protruding from the sclerite below spiracles is four, the same as in the first instar larva of *Tipula (Tipula) paludosa* (Meigen, 1830). However the reference to the drawing is erroneous; pictures of the two species are missing from the figure showing the stigma of the first instar larva of other species of tipulids (Savchenko 1983: 127–128, figs 67, 68).

Material, methods and terminology

All the material was collected by the author. Larvae were hand-sorted from soil samples (25x25x10 cm). In all, there were 10 samples selected on the shore near the water margin of Lake Sukhoe (five samples on the 22nd and 23rd of May and five on the 29th of May 2001). First instar larvae were obtained either in the laboratory, hatched from eggs laid by a captive female after mating, or were collected in their habitat after natural oviposition. The eggs were kept in refrigerators for six weeks at 5°C. The level of fecundity was estimated from mated specimens.

In the study locality parts of the shore of Lake Sukhoye near the water margin and the littoral zone, *T. subcunctans* is the only large species and may be the only species of Tipulidae in this particular place. This indicates that the field-collected larvae are of the species under study. The values of biomass indicate wet weight. The measurements were made using torsional balance.

The terms for the structures of larvae of Tipulidae as used in this paper are in accordance with those used by Oldham (1928), Chiswell (1956), Brindle (1959, 1960), Theowald (1967) and Teskey (1981).

Material examined

Tipula (Tipula) subcunctans Alexander, 1921

Imagines: Russia, Stavropolskiy Territory, Pyatigorsk, at light in room, 3 October 1991 (1♂); 6 November 1991 (1♂); on the wall of building, 24 October 1993 (2♂♂); broad-leaved forest on the SW slope of watershed ouval, river Podcumok basin, 19 October 1991 (1♂); Lake Sukhoe (43° 57' N., 43° 10' E.), in grass stand at shore near water margin, 8 October 2002 (8♂♂), 13 October 2002 (3♂♂, 12♀♀ in cop.); Lake Bolshoy Tambukan, small march, 200 m E of lake, 13 October 2002 (10♂♂, 2♀♀). Russia, Kabardino-Balkarian Republik, Bashil valley, 2000 m, 2 October 2005 (14♂♂, 2♀♀).

Larvae: Russia, Kabardino-Balkarian Republik, Lake Sukhoe (43° 57' N, 43° 10' E), shore near water margin, 21, 23 and 29 May 2001, 115 specimens from soil samples.

Tipula (Tipula) orientalis Lackschewitz, 1930

Imagines: Russia, Stavropolskiy Territory, Pyatigorsk (43° 03' N, 43° 02' E), 9 May 1997, water meadow of artificial lake, net-sweeping (7♂♂, 1♀). Russia, Dagestan, 2 km SW of village Zidjankazmaljar, 50 m, 2 May 2003 (1♂, 2♀♀); foot of SE slopes of Narat-Tyubinskiy chain, barkhan Sarykum, light trap, 4 May 2003 (1♂, 3♀♀); vicinity of village Butkasmaljar, 2 May 2003 (1♀), lower reach of Samur river, 2 May 2003 (1♂); 2 km SW of Dagestanskies Ognis, 2 May 2003 (1♀).

Results and discussion

Related species and their distribution

Of the 11 Palearctic species of the subgenus *Tipula* (Savchenko 1961; Oosterbroek 2009), apart from *T. subcunctans*, only two others, *Tipula (Tipula) orientalis* Lackschewitz, 1930 and *Tipula (Tipula) italica errans* Theowald, 1984, were found in the Caucasus. *T. subcunctans* is a widespread Palearctic species. The area of distribution of *T. orientalis* encompasses Central and Eastern Europe, Middle Asia and South-West Asia. In Russia, it is distributed in the southern European part,

including the lower Volga Basin, the Caucasus (Krasnodar Territory, the Black Sea Coast, Adygeya), Chechnya (Kyzlyar Region) and Dagestan. *T. orientalis* is known also in the Transcaucasia from Georgiya, Armeniya and Azerbaijan (Savchenko 1961). It is recorded here for Stavropolskiy Territory for the first time. The distribution of *T. italica errans* is restricted to the Central and Southern Europe, Turkey, Iran (Talysh), and the Transcaucasia (Armeniya, Georgiya, Azerbaijan) (Oosterbroek 2009).



FIGURE 1. The shore of Lake Sukhoe, Maliy Tambukan, 575 m, the North Caucasus, habitat of *T. subcunctans* Alexander, in spring.

Habitat and biology

T. subcunctans is a plain-subalpine species occurring as adults in late autumn. It is found at heights from 554 to 2100 m in Europe (Coulson 1959; Dufour 1986). In the Caucasus Mountains it usually occurs in plain and subalpine landscapes from 400m at Pyatigorsk up to 1800 m in Armenia (Savchenko 1961) and at 2000 m in the Central Caucasus (new data).

The species is of great interest owing to its stenotypic nature within the forest-steppe zone of the North Caucasus. Around Lake Sukhoe it is found within hygrophyte plant communities on gently sloping shores of salt pans and marshy areas. In spring the area is flooded with water (Fig. 1) but at the end of summer and in autumn-winter period the lake bed is exposed and becomes salt desert or solonchak (Fig. 2). Dominant species of vegetation in the habitats investigated are glassworts (*Salicornia europaea* L., *Tripolium vulgare* Nees) and on the lake margins *Epilobium hirsutum* L. is very common (Anatoliy Mikheev and Dmitriy Shilnikov, personal communication). Larvae were

found also on the shores of flood-plain lakes, former riverbeds and small rivers. In Switzerland, larvae of *T. subcunctans* occur in habitats that are temporarily inundated (Dufour 1986). According to Tjeder (1953), “The species frequents meadows and lawns ...was found in immense numbers on the golf course turf of Falsterbo in Skane [Sweden]. It apparently prefers soil, densely interwoven with roots of grasses. In wood and field the species has been found on shores of rivers and lakes, perhaps its original habitat”. These observations correlate well with our data mentioned above. According to Savchenko (1961), larvae can develop only in damp soil. It should be noted, however, that by Brindle (1960: 71) larvae of a few widely distributed species of *Tipula* s. str. “...can inhabit very different habitats, such as the common *T. paludosa* Mg., which is so abundant in pasture soils. These larvae also occur in a damp woodland soil, in marshy soils, and even in aquatic mosses in running water”. It has been observed that larvae of *T. subcunctans* are capable of surviving in water with a high concentration of sodium chloride; in Lake Sukhoye, it is over 32g per litre (Shinkarenko 1954). In May 2001, the abundance of larvae in certain parts of the littoral zone over an area of 20 m² is two specimens per 1 m².



FIGURE 2. The same view of the shore of Lake Sukhoe as in figure 1, in autumn.

The larvae *T. subcunctans* are supposedly phytophagous, as is *T. paludosa* (Ghiljarov & Semenova 1977). From new field observations, larvae can also feed on layers formed by algae and on filaments of algae that cover the bed and water surface of the lake (Manucharova 1954) as algal fragments occur in the contents of the gut of the larvae examined. In addition, it appears that larvae may be facultatively cannibalistic or necrophagous, considering that the parts of the spiracular lobes of the same species were also found in the gut contents.

The fourth instar larvae collected in the spring are probably from the previous year. This strategy is known from other groups of dipterans as well as tipulids (MacLean 1973; Lantsov 1982) which live in extreme conditions. A proportion does not pupate and remain as larvae in the soil until spring.

The habitats investigated are densely populated according to the data. The indices of larval abundance show they occur as aggregations at Lake Sukhoe. From 22nd and 23rd May 2004 the numbers from samples of 25x25x10 cm are as follows: on average 11.32±2.24 g/m² and 32±5.66 specimens/m²; maximum up to 19.2 g/m² and 52 specimens/m², respectively. An interesting fact is that several days later the biomass and the number of larvae of *T. subcunctans* decreased sharply to 5.9±2.1 g/m², 16±5.6 specimens/m². This can be explained by the migration of larvae deeper down due to an unfavourable dry period when the water surface of the lake fell and the upper layers of the soil on the shores became drier and tightened. In the sampling period *Tipula* larvae were the predominant element in the mesofauna (*sensu* Ghilarov 1975); other representatives of mesofauna were not numerous and included occasional specimens of earthworms, *Aporrectodea jassyensis* (Michaelsen, 1891), larvae of horseflies (Tabanidae), dolichopodids (Dolichopodidae), and soldier flies *Stratiomys singularior* (Harris, [1776]) (Stratiomyidae). Earthworms and Diptera larvae of other families constituted only a small part of the total biomass (less than 12.6% and 5.6%) and number (0.8 % and 22.2%) respectively.

Mass emergences of *T. subcunctans* (Fig. 3) were observed in mid-October when about 11 specimens per square meter were recorded in flight and mating and egg laying took place at 7°C . According to Savchenko (1961), the species can fly until early November when temperatures at the soil surface fall to 6° - 8°C below zero. This does not prevent adults from being active, provided the daytime temperatures stay above zero. Hollander (1975) demonstrated that in Netherlands this species "... occurs in smaller numbers and in more limited areas than *T. oleracea*, but especially so when compared to *T. paludosa*". He also stated that the species "...proved to be clearly univoltine, flying in late autumn". In the coastal communities of Lake Sukhoye, *T. subcunctans* coexists with typically halophilous species such as the limoniids *Symplecta (Psiloconopa) stictica stictica* (Meigen, 1818) and *Dicranomyia (Dicranomyia) sera* (Walker, 1848) as well as *Ephydra riparia* (Fallén, 1813), a shore-flies (Ephydridae). The first and the third of these species are particularly numerous.

Egg morphology and fecundity of females

The egg of *T. subcunctans* bears filaments (Hemmingsen & Theisen 1956; Hemmingsen & Jensen 1972). Dimensions of 20 eggs was investigated with the help of special measuring line, inserted in one of eyepieces of stereomicroscope. The length of filament is 6.86±0.16 mm. The length of eggs is 1.14±0.01 mm and width is 0.45±0.004 mm. The data on egg length and width by Jong (1925) are similar to these results, being 1 and 0.43 mm respectively. Fecundity in nine female specimens examined varied from 261 to 502 eggs, the average being 370±27. According to observations by Savchenko (1961, 1963), the fecundity of *T. subcunctans* can be higher, from 430 to 1475 eggs; 450 to 500 on average. Maercks (1941) pointed 455 eggs as an average fecundity of females. This species, along with *T. paludosa*, shows the highest fecundity level in the family. This feature can related to the conditions which cause high larval and egg mortality during winter and larval mortality during dry summer months.

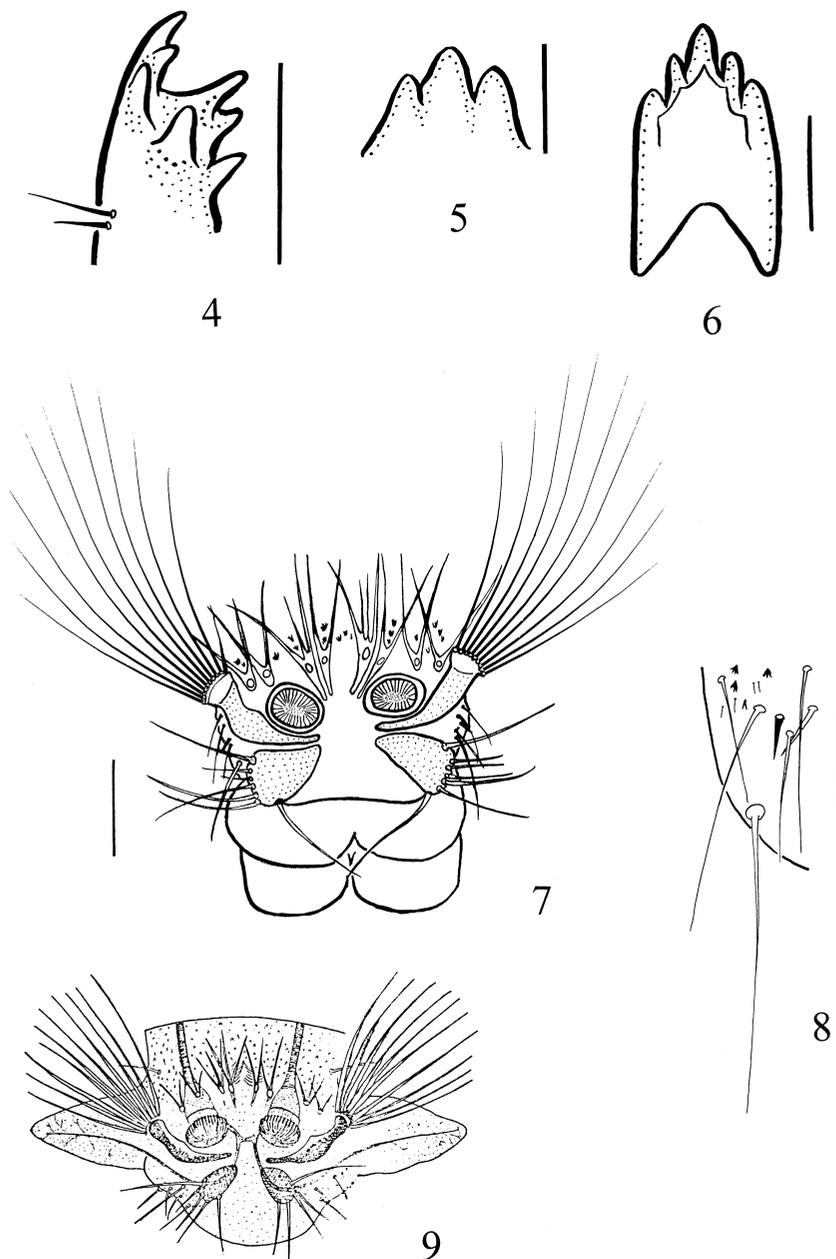
Morphology of first instar larvae

Head with well-developed upper jaws bearing seven teeth (Fig. 4), the distal of which with a smaller tooth on its inner surface. Labium and labrum are as in figures 5 and 6. The dorsal surface of the larva has distinct, sometimes faint light-brown transverse stripes formed by the amassment of tiny multi-tipped spicules. The ventral side of the body is whitish without distinct transverse welts. The thoracic segments have a higher density of spicules, and so their colour is darker. As in the first instar larvae of other species of Tipulidae, the spiracular disc (Fig. 7) is without dorsal lobes, having

only lateral and ventral ones. Lateral lobes short and wide, with nine long, large fan-like bristles with the middle ones longer. These large bristles arise from a narrow non-pigmented strip on the apex of a slightly expanded part of the lobe on which lays the basis of binate brown dark-pigmented triangular sclerites while the tops get gradually thinner; they stretch under spiracles and reach the middle of the spiracular disc and the basis of ventral lobes (fig. 7). Beneath the sclerites on the outer lateral side of anal field there are group of bristles (fig. 8); the number of delicate and large



FIGURE 3. Male of *T. subcunctans* Alexander on dead standing stems of *Epilobium hirsutum* L., the North Caucasus, shore of Lake Sukhoe, 10 October 2009.



FIGURES 4–9. Morphology of first instar larvae. 4–8—*T. subcunctans* Alexander (originals). 4—mandible, 5—labrum, 6—labium, 7—spiracular field, 8—bristles on lateral margin of spiracular disc between the triangular sclerites of lateral lobes and those of ventral lobes. 9—*T. paludosa* (from Selke 1936), spiracular field. Scale lines = 0.1 mm (4, 7), 0.05 mm (5, 6, 8).

ones varies. The sclerites of the ventral lobes of the spiracular disc are less pigmented but large, wide and triangular with five large and two smaller lateral bristles. The dorsal part of the spiracular disc, located between the lateral lobes, has eight small narrow triangular sclerites, the bases of which point towards the centre of the spiracular disc. Distally there are with 2 to 4 large bristles, varying between each sclerite. The largest sclerites are in the middle of the dorsal part of the spiracular disc between spiracles, the rest are between the spiracles and bases of the lateral lobes. Anal papillae are not pronounced. The distance between the oval spiracles is the same as the diameter of their central part. The anal field is represented by two pairs of strongly pronounced hemispherical structures. These are noticeable in those larvae that have been feeding and growing slightly and then submerged in boiling water for a short period. The length of the newly hatched larvae is from 2.1 to 2.4 mm and in well-developed larvae increases from 2.5 to 3.5 mm, the average length being 2.8 ± 0.12 mm.

According to Jong (1925), the lengths of first instar larvae of *T. subcunctans*, *T. oleracea* and *T. paludosa* are very similar to each other. It turns out that the spiracular field of first instar larvae of *T. paludosa* (Sellke 1936), differs from that of *T. subcunctans* as illustrated here by the number of long bristles on dorsal lobes, being 10 and 9 respectively (Fig. 9). The number of long bristles in outer edge below the ventral lobes is five in both species.

Morphology of fourth instar larvae

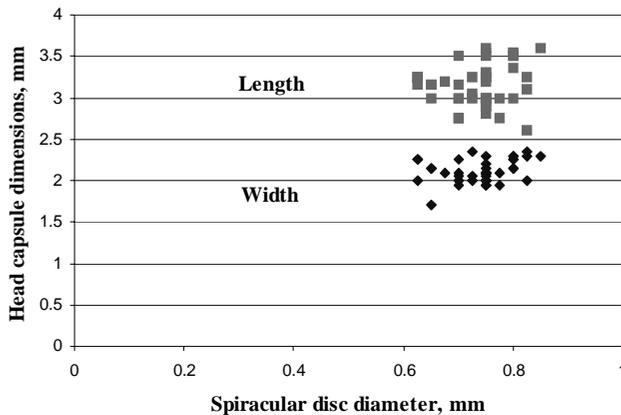
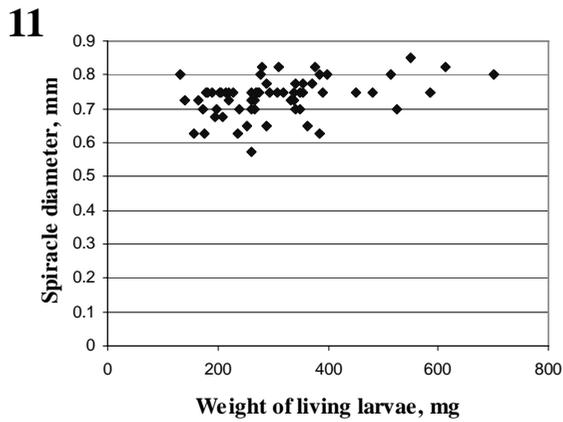
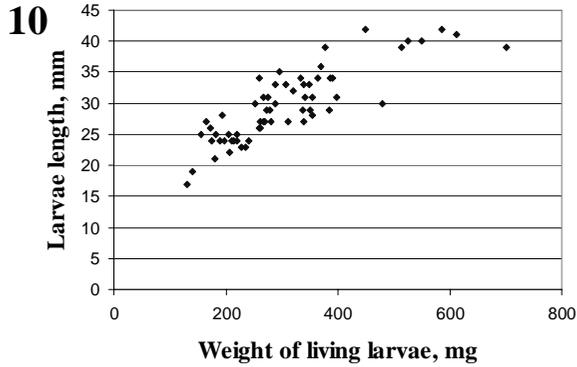
It is known that the best criterion for the estimation of the age of tipulid larvae is the diameter of spiracles (Hofsvang 1972; Hofsvang & Hagvar 1976; Lantsov 1982; Lantsov & Chernov 1987). This parameter does not overlap, or only slightly overlaps, with larval instars of contiguous age, whereas the weight and length of the larva are less conservative and do overlap with contiguous larval instars (Figs 10, 11, 12)

The data on spiracle diameter and head capsule length (Figs 13, 14) show that most of the larvae (71%) of *T. subcunctans* collected in the field belong to the fourth instar and the remainder (29%), to the third instar. In general 115 specimens of larvae were investigated. Using these data, the morphometry of the third and the fourth instar larvae of *T. subcunctans* is described (Table 1). The measurements conform fairly closely with those of Sellke (1936: 508), in which the length of the fourth instar larvae of *Tipula paludosa* is from 18–20 mm up to a maximum of 30 mm, head capsule width 1.18–2.00 mm and head capsule length 2–3 mm.

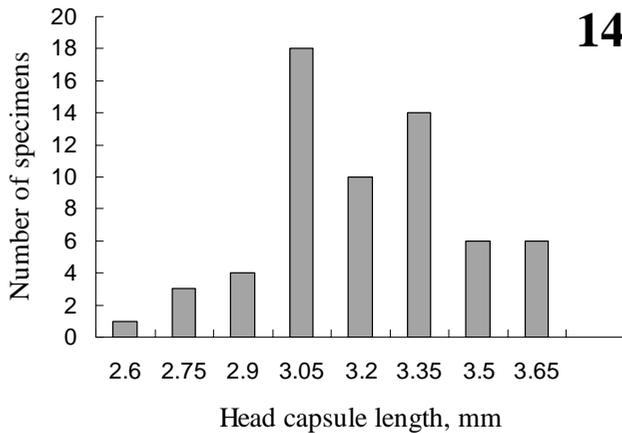
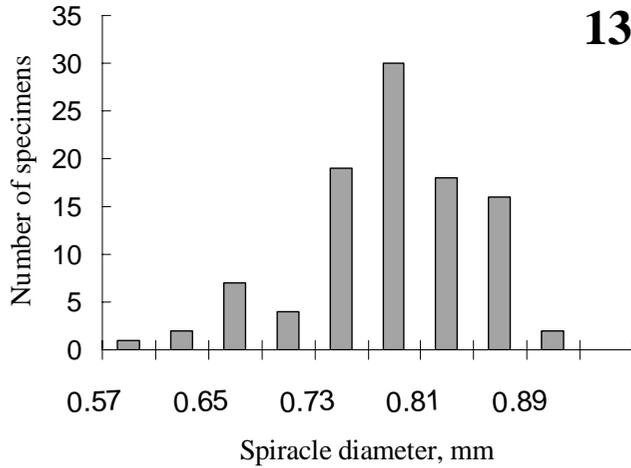
TABLE 1. Morphometry of third and fourth instar larvae of the North Caucasus population of *Tipula subcunctans*.

Larvae instar	Spiracle diameter, mm	Head capsule length, mm	Head capsule width, mm	Larvae length, mm	Weight of living larvae, mg
III	0.575–0.700	2.75–3.50	1.7–2.25	23–40	156–526
	0.665±0.009	3.086±0.044	2.081±0.032	28.44±1.124	270.77±22.01
IV	0.725–0.850	2.60–3.65	1.95–2.35	17–42	131–702
	0.764±0.001	3.195±0.039	2.14±0.017	30.02±0.92	322.52±19.16

In studying the field-collected fourth instar larvae, it appears that they can be divided into groups as morph I (~45%) (Fig. 15), morph II (~45%) (Fig. 16) and the third, intermediate group without the clear distinguishing features which characterize the first and second morphs (9.7%) (Table 2). Morph II is very similar to those as showed by Brindle (1959) (Fig. 17).



FIGURES 10–12. Correlations between length and weight (10), spiracle diameter and weight (11), spiracle diameter and head capsule dimensions (12) of larvae of *T. subcunctans* Alexander.



FIGURES 13, 14. Frequency distribution of spiracle diameter (13) and head capsule length (14) of larvae of *T. subcunctans* Alexander.

Among the morphological characters of the fourth instar in Table 1 the diameter of spiracles is relatively stable and apparently does not overlap with that of instar 3, whereas all other values do overlap between the two instars.. The presence and the size of anal papillae (tracheal gills) are not always stable. Large larvae with the length exceeding 33 mm (33– 42 mm) and weighting more than 450 mg (450–702 mg) usually belong to the second morphotype. Possibly, the field-collected larvae include a proportion of the fourth instar larvae from the previous year that did not pupate in the autumn. It is known that under unfavourable conditions many insects, including tipulids (Lantsov 1982), adopt this strategy (see above).

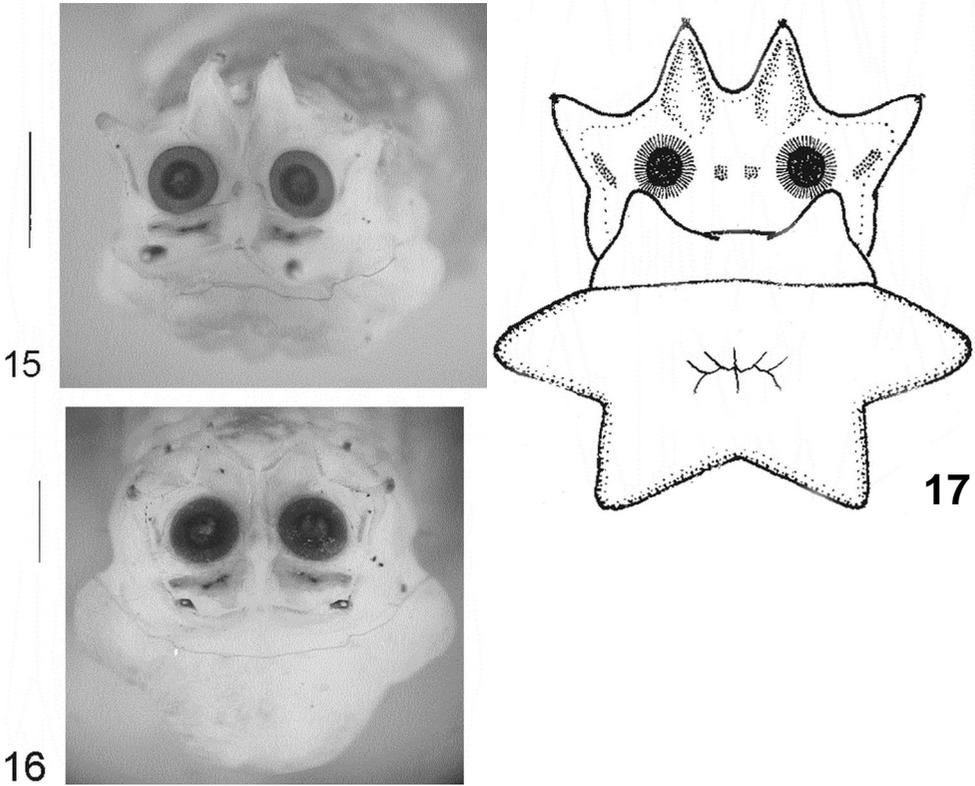
Some data on the morphology and biology of fourth instar larvae of *T. subcunctans* were available previously (Jong 1925; Sellke 1936; Maercks 1941; Brindle 1959). A diagram of the spiracular field of fourth instar larvae of *T. subcunctans* appeared for the first time in Brindle (1959) with the analysis of larval morphology in comparison with those of *T. paludosa* and *T. oleracea*. Brindle (1959: 177) suggested "... the most likely explanation of the previous inability to separate

TABLE 2. Characters of morphs of the fourth instar larvae in the North Caucasus population of *T. subcunctans*.

Character	Morph I	Morph II
Anal papillae	Not prominent; only as slightly evident upper pair (Specimens occur with anal papillae less prominent)	Prominent, at least upper pair distinct
Dark markings between spiracles	Absent or only faintly observable (Specimens occur without any pigmentation between spiracles or dark markings or spots may be hidden in folds; sometimes pigmentation present as a U-shape, bracket-shaped or inclined narrow lines)	Two small dark markings or mostly narrow grey spots, more or less prominent
Spiracle diameter, mm	0.725–0.850	
Head capsule length, mm	2.60–3.55	2.75–3.60
Head capsule width, mm	1.95–2.35	1.95–2.35
Larvae length, mm	17–32	27–42
Weight of living larvae, mg	140–385	252–702

the larvae into the three species is that the larvae are dimorphic". The new data presented here are in general agreement with this assumption. Characters noted by Brindle (1959), such as the pair of anal papillae (tracheal gills) and pigment spots between spiracles are present in the North Caucasian population (Figs. 16, 17). However, they are found mainly in large fourth instar larvae and are not always clearly expressed. Most larvae were found aggregated in soil samples, occurring in saturated swampy mud although some specimens were in water (as mentioned above). These two groups have differences in morphology, as those found in the swampy mud are of morph I (Table 2) and are close to *T. paludosa* as illustrated by Chiswell (1956: 470) but without prominent anal papillae. Another one found in water is of morph II and is similar to those referred to as *T. subcunctans* in Brindle (1959) (Fig. 17). The presence of these morphs can explain the fact, that the larvae of these sibling species were regarded as practically indistinguishable (Chiswell 1956; Sellke 1936). Characters used by Brindle (1959) for the fourth instar larvae of *T. subcunctans*, namely, all four papillae elongated and prominent dark markings between the spiracles, are found in the North Caucasus larvae of the species (mostly in older and over-wintered specimens), but not always pronounced.

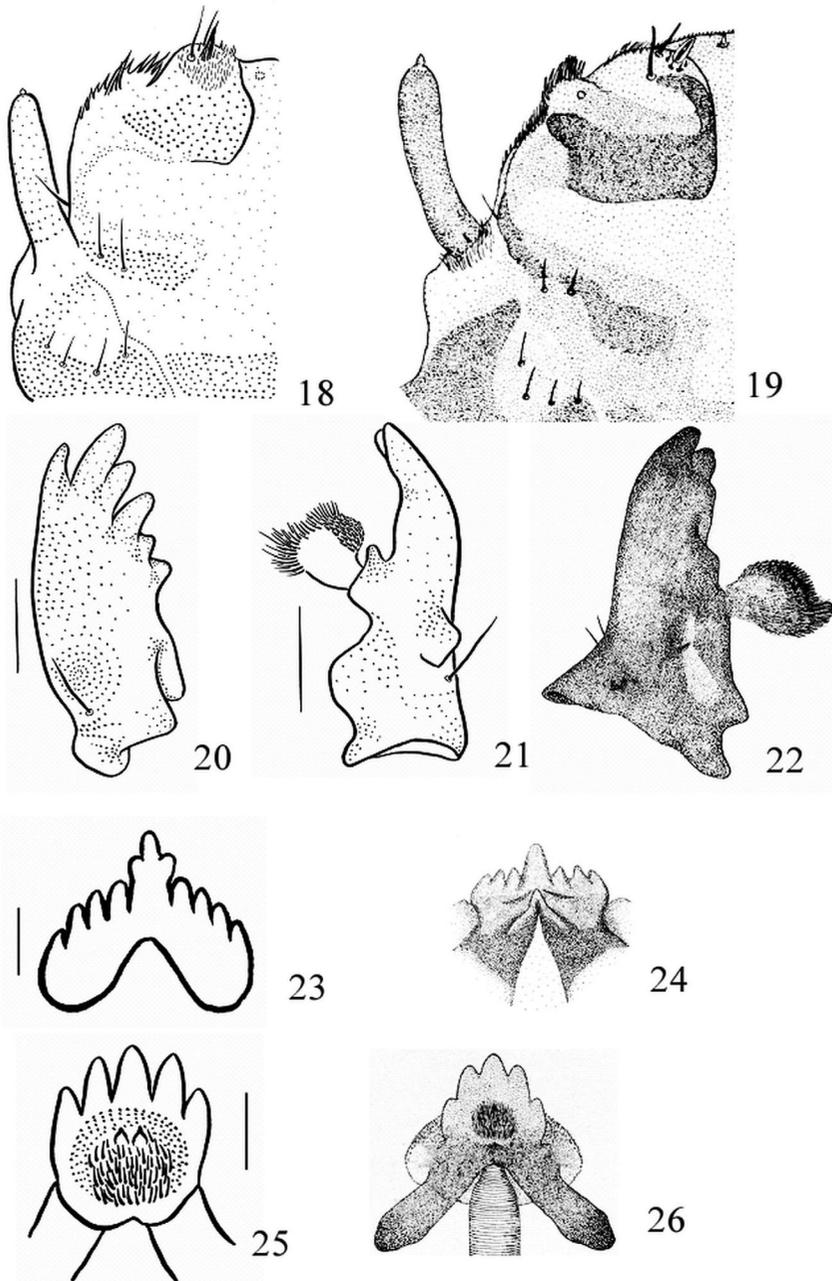
Morphology of mouth parts of fourth instar larvae of *T. subcunctans* have the same shape in both morphs, mentioned above (Figs. 18, 20, 21, 23, 25). According to Pjotr Oosterbroek (personal communication) the fourth instar larvae of close species *T. paludosa* and *T. subcunctans* are different in morphology of mouthparts. The differences between mouthparts of *T. subcunctans* (the North Caucasus population) and those of *T. paludosa* (as showed by Oldham 1928) are obvious in forms of mentum of labial plate (Figs. 23, 24), less in the shape of hypopharynx (Figs. 25, 26) and the mandible (Figs. 20, 21, 22). Differences in morphology of clypeo-labral region of the head capsule concern the presence of four small spicules at the base of thick spine located distally in *T. paludosa* (Fig. 19) and their absence in *T. subcunctans* (Fig. 18).



FIGURES 15–17. Morphology of fourth instar larvae of *T. subcunctans* Alexander 15–16— Spiracular field of morph I (15) and morph II (16) (original). 17—Spiracular field from Brindle (1959). Scale lines = 1 mm (15), 0.75 mm (16).

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FIGURES 18–22. Morphology of fourth instar larvae of *T. subcunctans* Alexander (18, 20, 21, 23, 25-originals) and *T. paludosa* Meig. (19, 22, 24, 26-from Oldham, 1928). 18, 19-clypeo-labral region of the head capsule, dorsal view; 20, 21-right mandible (20, - dorsal view, 21- ventral view); 22-left mandible (dorsal view); 23, 24-mentum of labial plate, ventral view; 25, 26-hypopharynx, ventral view. Scale lines = 0.3 mm (18, 20, 21), 0.25 mm (23, 25); x 60 (19, 22, 26), x70 (24).

References

- Brindle, A. (1959) Notes on the larvae of the British Tipulinae (Dipt., Tipulidae). Part 6. The larvae of the *Tipula oleracea* group. *Entomologist's Monthly Magazine*, 95, 176–177.
- Brindle, A. (1960) The larvae and pupae of the British Tipulinae (Diptera: Tipulidae). *Transactions of the Society for British Entomology*, 14, 63–114.
- Byers, G.W. (1958) Species recognition in immature crane flies (Diptera, Tipulidae). *Proceedings 10th International Congress of Entomology* (1956), Montreal, Volume 1, pp 131–136.
- Coulson, J.C. (1959) Observations on the Tipulidae (Diptera) of the Moor House Nature Reserve Westmorland. *Transactions of the Royal Entomological Society of London*, 111, 157–174.
- Chiswell, J.B. (1956) A taxonomic account of the last instar larvae of some British Tipulidae (Diptera: Tipulidae). *Transactions of the Royal Entomological Society of London*, 108, 409–486.
- Dufour, C. (1986) *Les Tipulidae de Suisse (Diptera, Nematocera)*. Documenta Faunistica Helvetiae, 2, Edité par le Centre suisse de cartographie de la faune, Neuchatel, 187 pp.
- Ghilarov, M.S. (1975) Taking censuses of larger invertebrates (mesofauna). *Metody pochvenno-zoologicheskikh issledovaniy. [Methods of soil zoological studies.]*, Nauka, Moscow, pp. 12–29. (In Russian).
- Ghilarov, M.S. & Semenova, L.M. (1977) The peculiarities of alimentary system of soil larvae of insects with different mode of feeding. *Adaptatsiya pochvennyh zhivotnyh k usloviyam sredy. [Adaptation of soil animals to environments]*. Nauka, Moscow, pp. 49–54. (In Russian).
- Hemmingsen, A.M. & Theisen, B.F. (1956) The inheritance of terminal egg-filaments in fertile hybrids of *Tipula paludosa* Meigen and *Tipula czizeki* de Jong. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København*, 118, 15–32.
- Hemmingsen, A.M. & Jensen, B. (1972) Egg characteristics and body size in crane flies (Diptera: Tipulidae) with comparative notes on birds and other organisms. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København*, 135, 85–127.
- Hollander, J.D. (1975) The phenology and habitat of the species of the subgenus *Tipula* Linnaeus in the Netherlands (Diptera, Tipulidae). *Tijdschrift voor Entomologie*, 118 (3–4), 83–97.
- Hofsvang, T. (1972) *Tipula excisa* Schum. (Diptera, Tipulidae), life cycle and populations dynamics. *Norsk Entomologisk Tidsskrift*, 19, 43–48.
- Hofsvang, T. & Hagvar, S. (1976) Density and composition of crane-fly larvae (Diptera, Tipulidae) from an alpine wet meadow at Sugstiv Hardangervidda. South Norway. *Norwegian Journal of Entomology*, 23, 41–43.
- Jong de, W.H. (1925) Een studie over emelten en hare bestrijding. *Verslagen en mededelingen van de Plantenziektenkundige Dienst*, 42, 1–126.
- Lantsov, V.I. (1982) Adaptive peculiarities of the life-cycle of the arctic crane fly *Tipula carinifrons* (Diptera, Tipulidae). *Ecology*, 1, 71–76. (In Russian).
- Lantsov, V.I. & Chernov, Y.I. (1987) Tipuloidnye dvukrylye v tundrovoi zone [*Tipuloid crane-flies in the tundra zone*]. Nauka, Moscow, pp. 176. (In Russian).
- Lantsov, V.I. (2004) The tipulomorphous dipterans (Diptera, Tipulomorpha) in the basin of lakes Maliy and Bolshoy Tambukan. *Problems of ecology of mountain territories*. In: Proceedings of the Institute of Ecology of Mountain Territories of Kabardino-Balkarian Scientific Centre of Russian Academy of Science. Nalchik, pp. 62–68. (In Russian).
- MacLean, S.F. (1973) Life cycle and growth energetics of the Arctic crane-fly *Pedicia hanaui antennata*. *Oikos*, 24, 434–443.
- Maercks, H. (1941) Über Biologie und Schädlichkeit der Herbstschnake (*Tipula czizeki* de Jong). *Arbeiten über physiologische und angewandte Entomologie aus Berlin-Dahlem*, 8, 197–205.
- Manucharova, T.A. (1954) Rastitelnost ozer Bolshoy i Maliy Tambukan. [Vegetation of lakes Bolshoy and Maliy Tambukan]. In: *Tambukanskoe ozero I ego tzelebnaya gryaz. [The Tambukan Lake and its therapeutic mud]*. Stavropol, pp. 123–131. (In Russian)
- Oldham, J.N. (1928) On the final larval instar of *Tipula paludosa* Meigen and *Tipula lateralis* Meigen. *Proceedings*

of the Royal Physical Society of Edinburgh, 21, 217–252.

- Oosterbroek, P. (2009) Catalogue of the Craneflies of the World (CCW). Available from <http://ip30.eti.uva.nl/ccw/> (latest update: 3 September 2009).
- Savchenko, E.N. (1961) *Crane-flies (Fam. Tipulidae), Subfam. Tipulinae, Genus Tipula L., (part 1)*. Fauna USSR, New Series N 79, Nasekomye dvukrylye [Diptera], 2(3), 487 pp. Mosc.- Len., Izdatelstvo “Nauka” [Publishing house of Academie of Sciences of the USSR]. (in Russian).
- Savchenko, E.N. (1981) Family Tipulidae, crane-flies or long-legged flies. *Insects and ticks as pests for crops*. Vol. IV. *Hymenopterans and dipterans insects*. Nauka, Leningrad, pp 57–63. (In Russian)
- Savchenko, E.N. (1983) *Crane-flies (Fam. Tipulidae), Introduction, and beginning of systematic part. Subfam. Dolichopezinae, subfam. Tipulinae (start)*. Fauna USSR, New Series N 127, Nasekomye dvukrylye [Diptera], 2(1–2), 586 pp. Leningrad, “Nauka” Leningradskoe otdelenie. [Publishing house of Academie of Sciences of the USSR]. (in Russian).
- Sellke, K. (1936) Biologische und morphologische Studien an schädlichen Wiesenschnaken (Tipulidae, Dipt.). *Zeitschrift für wissenschaftliche Zoologie (A)*, 148, 465–555.
- Sellke, K. (1937) Beobachtungen über die Bekämpfung von Wiesenschnakenlarven (*Tipula paludosa* Mg. und *Tipula czizeki* de J.). *Zeitschrift für angewandte Entomologie*, 24, 277–284.
- Shinkarenko, A.L. (1954) Hydrochemistry of the Tambukan lake. In: *Tambukanskoe ozero I ego tzelebnaya gryaz. [The Tambukan lake and its therapeutic mud]*. Stavropol, 27–36. (In Russian).
- Teskey, H.J. (1981) Morphology and terminology—larvae. In: McAlpine, J.F. et al. (Eds.), *Manual of Nearctic Diptera*. Volume 1. Monograph No 27. Research Branch Agriculture Canada. pp. 65–88.
- Theowald, B. (1957) Die Entwicklungsstadien der Tipuliden (Diptera, Nematocera), insbesondere der Westpalaearktischen Arten. *Tijdschrift voor Entomologie*, 100, 195–308.
- Theowald, B. (1967) Familie Tipulidae (Diptera, Nematocera). Larven and Puppen, *Bestimmungsbücher zur Bodenfauna Europas*, 7, 1–100.
- Tjeder, B. (1953) The identity of *Tipula oleracea* L. *Opuscula Entomologica*, 18, 111–115.

