

## A crane-fly larva (*Tipula juncea* Meigen) living in blown sand.

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Most tipulid eggs shrivel if not kept moist, and few tipulid larvae live in dry localities. For instance, Rogers (1933, p. 23) found that out of 18 types of inland locality in northern Florida, the two driest were not inhabited by any stage of any species. However, the palaeartic *Tipula juncea* Meigen oviposits in sometimes apparently rather dry sandy soils, for instance even blown sand, by insertion of the entire abdomen into the sand, so that the eggs are laid at a distance below the surface, which is likely to ensure a sufficiently high relative moisture even though the absolute content of moisture may be low (Hemmingsen, 1952, p. 370—385, notably p. 379—380; also 1956, p. 270—275).

Still, in captivity the species prefers wet sand for oviposition (Hemmingsen, 1952, p. 430); and Savchenko (1956, p. 140) describes as its biotopes moist sandy soils at meadows and ponds in woods, and shrubberies along rivers and lakes beaches. Where I have found the species and where I have seen it oviposit in nature the sand would, however, generally be rather dry at least in the surface (dune heath and fire-breaks in dune forest in Western Jutland and North Sealand).

It seems likely that other species of the *Tipula juncea*-group are adapted to similar dry biotopes, for the shovel-shaped cerci characteristic of the group are evidently adapted to deep ovipository borings, and at least one of the species, *Tipula pribilofensis* Alexander is reported from sand dunes ("Tolstoj dunes") in the Pribilof Islands (Alexander, 1923).

In a previous paper (Hemmingsen, 1956, p. 248) a survey of the geographical distribution of the *T. juncea*-group was attempted. It should be supplemented with *T. platyglossa* Alexander 1936 and *T. timptonensis* Savchenko 1956 from palaeartic Asia.

In a survey in the Ukrainian language of the palaeartic species of the group Savchenko (1956) has proposed for it the subgeneric name *Odonatisca* (from the superficial resemblance of female *T. juncea* to small *Odonata*). He reduces *T. juncea*, *T. mystica* Alexander 1924, and *T. platyglossa* to being three geographical subspecies of one species, *T. juncea*, and thinks that *T. longicauda* Matsumura is a synonym of *T. mystica*. While Lackshewitz (1936, p. 298) reports *T. juncea* no further east than European Russia, Savchenko quotes it (*T. j. juncea*) as occurring not only in the whole of Europe, except in the extreme north and perhaps in the south, but also in S. W. Siberia to the Altai and east to S. perhaps also N. Yakutia. South of the easternmost part of its range it is replaced by *T. j. platyglossa* in the Baikal area, west to Krasnoyarsk, north almost to Yakutia, east to the Amur region; and south of the Sayan, in at least part of Mongolia. In the Far East the third subspecies, *T. j. mystica* is known from the Sovjet Coastal Provinces, Sakhalin and Hokkaido, but may perhaps extend somewhat further south.

The larvae of the group are unknown (Savchenko, 1956, p. 132). The pupa of *T. juncea* was described, on the basis of both sexes, by Theowald (1957, p. 279).

The posterior end of larvae of *Tipulinae* is usually truncated in the shape of a spiracular disc bearing the two spiracles and surrounded by a number of fleshy lobes usually 6 arranged in dorsal, lateral, and ventral pairs and often adapted to suspension from a water surface film. In species living in free water the lobes may be provided with strikingly long hairs, which especially

ensure the attachment to the water surface film. I have seen this particularly pronounced in the (first instar) larva of *Tipula saginata* Bergroth which oviposits in moss on stones in the midst of streams (Skäralid and Klöva Hallar, Scania, in May-June). Yet, the lobes are present also in

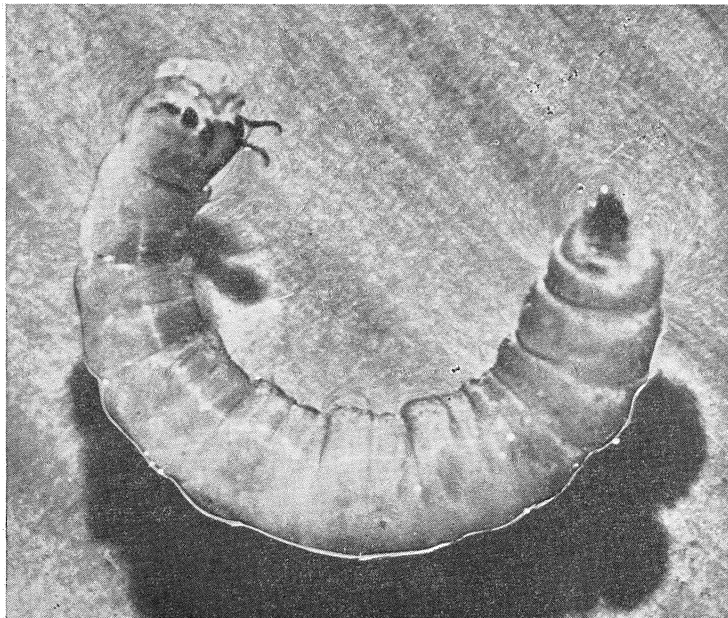


Fig. 1. Larva photographed in water. Length 22—29 mm according to degree of stretching.

a number of species that live in less saturated substrates such as forest soil or wood. In some of the larvae living in decayed wood they are rudimentary.

It seemed of interest, therefore, to know to what extent such lobes were developed in a tipulid larva living in a substrate such as blown sand where it would not have to place its spiracular disc against any water surface film, and where there may be expected to be some

danger of desiccation even though the sand may usually be rather moist except near the surface.

Thorough and repeated searching about mid-May by digging and sifting sand in a locality where imagines of *Tipula juncea* were known to have occurred from the end of May to about the beginning of August in the preceding years (fire breaks of the dune forest of Tisvilde Hegn in North Sealand), yielded only (18. V. 1954) one nearly full-grown tipulid larva and one tipulid pupa at a depth of about 15—20 cm. They are illustrated in figs. 1—3. The pupa was *Tipula juncea* Meigen, as kindly identified by Dr. Br. Theowald, Amsterdam. The larva during movement in water measured about 26 mm in length and 3.6 mm in diameter. It was yellowish white. A dense cover of longitudinally directed dark hairs produced in certain lights a brilliant lustre. There were also single thin bristles toward the sides; and above, small black points irregularly ar-

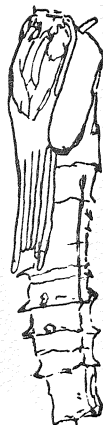


Fig. 2. Pupa. Length 18.5 mm.

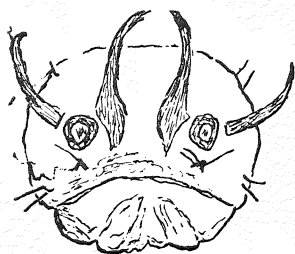
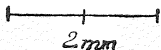


Fig. 3. Spiracular disc of the larva shown in Fig. 1.

ranged. The head capsule was dark. No intestinal content could be discerned.

The very characteristic spiracular disc on the larval skin still attached to the pupa when it was found, indicated that the pupa was of the same species as the larva, the spiracular disc of which is shown in fig. 3. It will be seen that the dorsal and lateral lobes of the spiracular disc are not fleshy as in most tipulids but are heavily sclerotized as long anteriorly curved horns. Unfortunately the larva perished in my absence during an attempt at hatching.

That the larva in question actually belonged to the species *Tipula juncea*, was checked by rearing larvae hatched from eggs laid by *T. juncea* females. Following a method kindly demonstrated to me by Professor Hans Bauer and Miss Liselotte Richter, Wilhelmshaven, on my visit there in 1953, the larvae were fed on moistened *Urtica* leaf powder as obtainable from a drug store (*Herbae Urticae*). The larvae emerged from the eggs after 10—14 days, but they developed very slowly. Larvae preserved at various body sizes could be arranged in three groups according to body size, size of the head capsule and type of spiracular disc (see table and figs. 4—7).

The head capsules and the spiracular discs have practically one appearance within all larvae of 2.7—7 mm body length (fig. 5 and 7 a-b), and a somewhat different appearance within those of 7—9 and 26 mm body length (fig. 6, 7 a-c, and 3). Remarkably enough [the bifurcate horny appendages of the spiracular disc of the first two size groups (fig. 7 a and b) are smallest in the larger of these two groups. Of the spiracular discs in the 6 larvae in the 3rd size group, 2 are as pictured in fig. 7c, while two are as shown in fig. 7d; and two as in

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Fig. 4. Preserved larvae of *Tipula juncea* Meigen reared on *Urtica* leaves. Body lengths: a: 2.7—4.5 mm; b: 5—7 mm; c: 7—9 mm. Within each of the stages a, b and c the left larva presents a dorsal view; the middle larva, a lateral view; and the right larva, a ventral view.

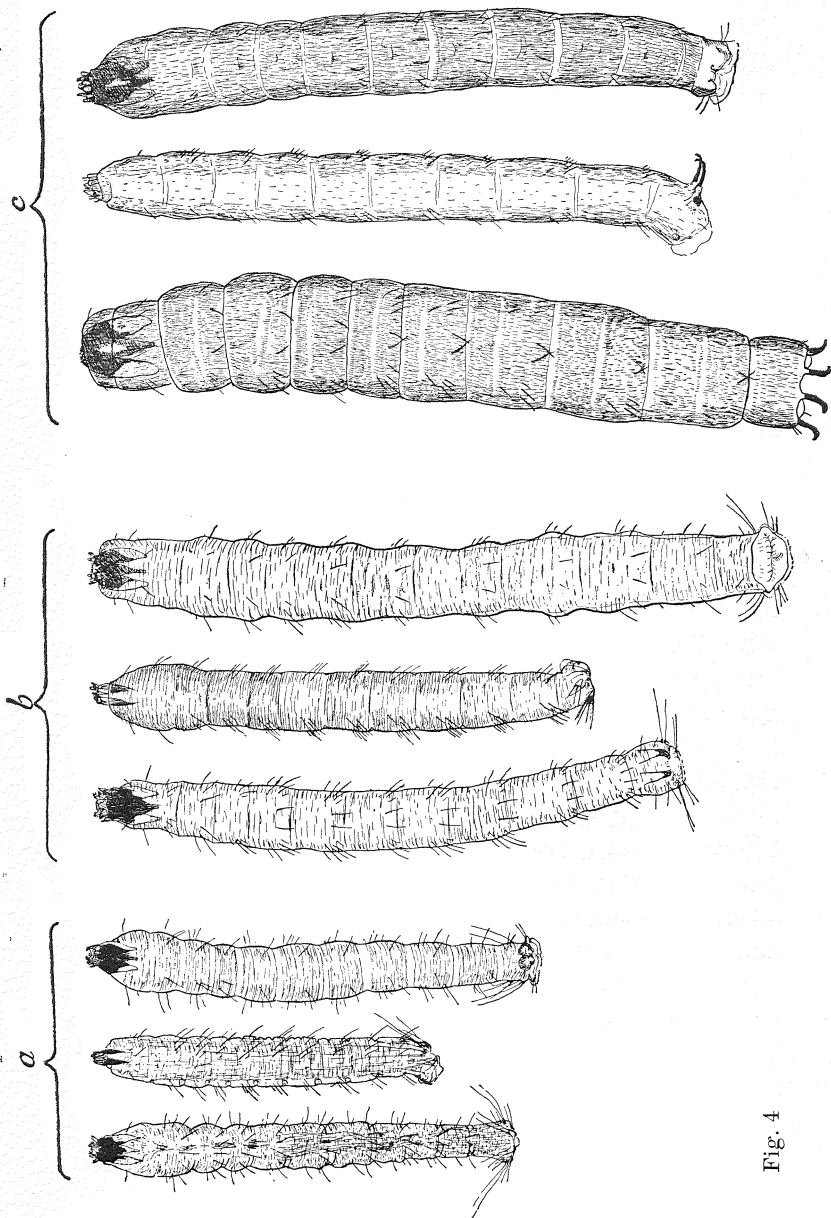


Fig. 4

4\*

**Table.**  
Available larval stages of *Tipula juncea* Meigen.

Length of larvae in mm	Head capsule breadth in mm		Number of larvae	Fig. No.	
	Majority of larvae	Mean		Whole larvae	Spiracular disc
2.7—4.5	0.22—0.28	0.25	25	4 a	7 a
5—7	0.31—0.37	0.36	27	4 b	7 b
7—9	0.38—0.63	0.50	6	4 c	7 c-e
26	1.31		1—(2*)	1	3

\*) Larval skin attached to pupa shows head capsule and spiracular disc.

fig. 7 e. Fig. 7 e represents a larva preserved in November from eggs laid the same summer: June-July 1955. It will be seen that the spiracular disc in fig. 7 e is very much like the one in fig. 3 of the larvae found in nature with the exception that the rudimentary ventral lobes are placed more laterally (as also in fig. 7 d) than in fig. 3 apparently joining the lateral pair of setae seen in fig. 3. Now, in fig. 7 c though the dorsal and still more the lateral horny lobes are very poorly developed, the rudimentary ventral lobes are actually placed as in fig. 3 below the spiracles with some hairs in a more lateral position. There is thus very much to indicate that the larva represented in figs. 1 and 3 was actually *Tipula juncea*.

Within the third size group there is rather a wide variation in breadth of head capsule (see table), and the difference between the three types of spiracular discs (figs. 7 c, d and e) within the same group is perhaps correlated with differences in head capsule breadths. For the purpose of discussion we shall, however, at least provisionally consider the third size group as one entity.

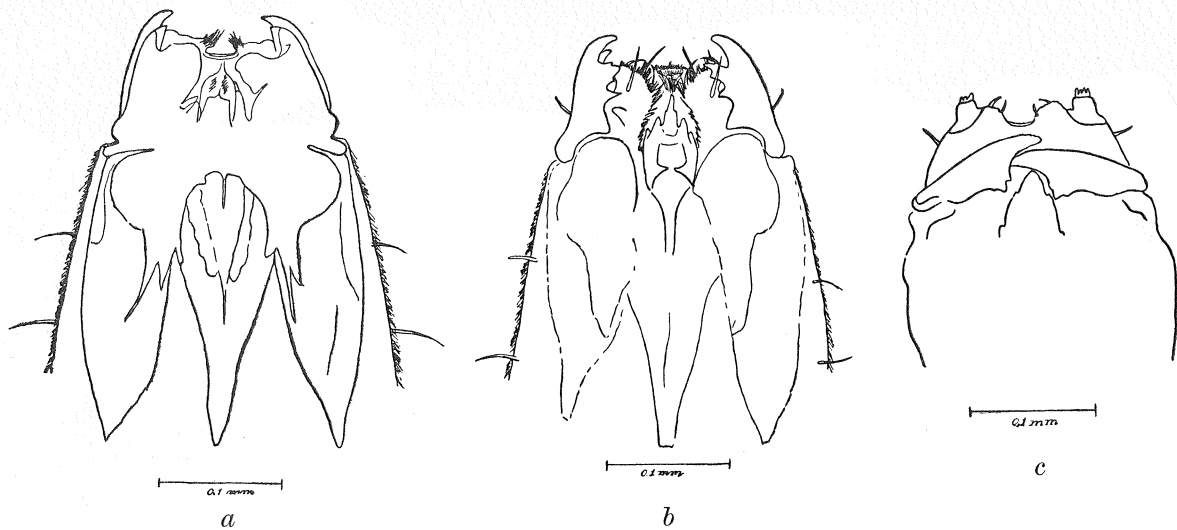


Fig. 5. Head capsules of the smallest size group of *Tipula juncea* larvae (2.7—4.5 mm body length). Cleared in euparal (a and b) or canada balsam (c).

a. dorsal, b. ventral views of same larva; c. ventral view of another larva with adducted mandibles, so that the antennae are visible.



It is stated as a general rule that there are 4 larval instars in *Tipula* (Hennig, 1950; Brauns, 1954). If this applies also to *T. juncea*, the question arises whether the four instars might be represented by the four horizontal lines in the table; by figs. 4 a, b, c and fig. 1 for the whole

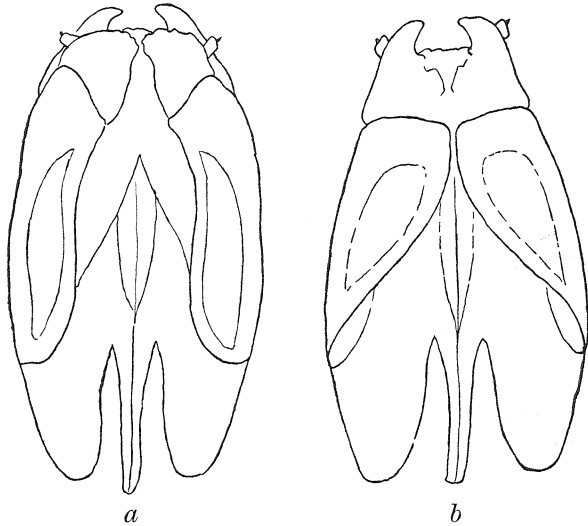


Fig. 6. Head capsules of full-grown larva. a. dorsal, b. ventral view. Schematic drawing based on head capsules from remnants of full-grown larva, on larval skin attached to pupa, and on stage c. Should perhaps have been a little broader relative to its length. Normal breadth about 1.3 mm.

larvae, and by figs. 7 a, b, c-e, and fig. 3 for the spiracular discs.

According to Dyar (1890) the insect head-width follows a regular geometrical progression in successive instars (Dyar's law; cf. Imms, 1957, p. 230). Figures given by De Jong (1925, p. 26, 30, 42 and 45) for *Tipula oleracea* "L. 1758", *T. paludosa* Mg., *Pales maculata* Mg. and *T. vernalis* Mg., and by Sellke (1936, table on p. 508) for *Tipula paludosa* Meigen and *Tipula czizeki* De Jong show

that the "law" applies also to the 4 larval stages in these tipulids. It will be seen from the table, however, that in *T. juncea* the increase in mean breadth of the head capsule from one size group to the next agrees with Dyar's law only from group 1 to 2, and from 2 to 3, whereas the difference between the size groups 3 and 4 in the

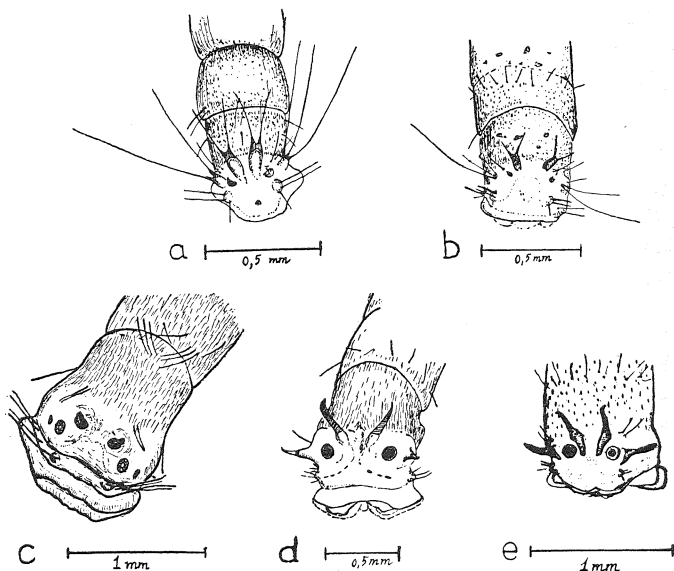


Fig. 7. Spiracular discs of young larvae of *Tipula juncea* Meigen reared on *Urtica* powder. Body lengths: a: 2.7—4.5 mm; b: 5—7 mm; c, d and e: 7—9 mm.

table would require two other instars between them to conform with Dyar's law. In this connection it is irrelevant that the ratio of width of the insect head capsule in one instar to that in the preceding instar may not be really constant but slightly changing throughout development (cf. Bliss and Beard, 1954, and Imms, 1957; both with references).

Compared with the body lengths at the 4 larval stages of the other *Tipula* species just mentioned growth in the

3 first size groups of the larvae under consideration is much retarded. The three types of spiracular discs (figs. 7c-e) within the third size group may possibly represent different degrees of retardation within one instar. It seems therefore possible that the head capsule breadths of the 3 first stages, reared on *Urtica* powder, have attained much smaller sizes than they do under natural conditions on a possibly more adequate diet; rather than that 2 instars should be missing.

Sclerotization of the dorsal and lateral lobes of the spiracular disc as four curved horns as in the larvae of *T. juncea* is found also in the larvae of *Tipula* (*Lunatipula*) *livida* v. d. Wulp (Savchenko, 1954, fig. 19 on p. 625; Chiswell, 1955; Theowald, 1957, p. 257—259), the related Canarian *T. (L.) lesnei* Pierre (Hemmingsen, published 1958), and possibly *T. (Lunatipula) recticornis* Schummel (Theowald, 1957, p. 258—260), as well as an unknown North American species (Alexander, 1920, p. 1016, and plate XCVI, fig. 535). *T. livida*, *T. lesnei* and *T. recticornis* all belong to the *Tipula livida*-group within the subgenus *Lunatipula*. The statement by Beling, (1878, p. 34—35) as repeated by Czizek (1913, p. 160—161) and others, that four such horns occur in the larva of *Tipula selene* Meigen, is due to confusion with *T. livida* (Chiswell, 1955, p. 127; Theowald and Mannheims, 1956, p. 252). The horned larvae described by Beling as *T. selene*, but which were *T. livida*, were found in black wood mould on decayed beech wood and in vegetable mould underneath beech leaves. Savchenko found the larvae of *T. livida* at the base of trees in dry broad-leaved and mixed woods. Chiswell (1954, 1955) found them in the surface of beech forest soil under loose, damp moss and in the top inch or so of moist leaf mould and soil in woods. And Theowald found them in the layer of dead leaves ("Streuschicht") under birch bushes. The larvae of *T. lesnei* live in soil which is often in danger

of being dried up (Hemmingsen, published 1958). The larvae supposed by Theowald to be of *T. recticornis* and according to him described by Savchenko as *T. fascipennis*, were found in the layer of dead leaves in but little moist woods and under bushes (Savchenko). The North American larva mentioned was found beneath a stone in a field.

Near approaches to the structure of the larvae of *T. juncea*, *T. livida*, *T. lesnei* and the presumed *T. recticornis* are to be seen in other species of the subgenus *Lunatipula*, such as *T. brevispina* Pierre and *T. selene* Meigen, in which the apical half of each dorsal lobe of the spiracular disc is entirely sclerotized and hook-like (Chiswell, 1956, p. 424; also his figs. 70—71). Chiswell (1956, p. 454 and 457) found the larva of *T. brevispina* in moist woodland soil or under bark or in debris on decaying logs and stumps; and that of *T. selene*, in debris inside the hollow trunk of a willow. Dr. B. Mannheims, Bonn (*in litt.*) has bred *T. selene* from a larva from decayed beech wood; and Theowald (1957, p. 257) found larvae of this species in decayed wood and moss at the base of a dead birch. Even in the larvae of *T. (Vestiplex) scripta* Meigen, *T. (L.) lunata* L., *T. (L.) cava* Riedel, and *T. fascipennis* Meigen the tips of the anteriorly curved conical dorsal lobes are sclerotized (Savchenko, 1954, figs. 13 and 17; Chiswell, 1956, p. 452 and 454, and figs. 68 and 71; Theowald, 1957, p. 249—256). The larvae of *T. scripta* and *T. lunata* live in moist soil and leaf mould in woods or under hedges; and those of *T. cava* and *T. fascipennis* have been found for instance in old cow-dung and under grass.

Also a North American species, *Tipula (Lunatipula) australis* Doane has horn-like structures in the position of the dorsal pair of lobes, the lateral lobes being also strongly sclerotized on their posterior (or ventral) surface. Fourth instar larvae of this species were taken in

Douglas county, Kansas, 15 miles south of Lawrence in February, March and April in loose, organic, sandy soil, fairly damp, at the base of a sandstone cliff in a ravine. Under these conditions there would be occasions when the soil would be quite wet, but in general it was only damp. Also in some other North American (unknown) species the lobes are at least partly horn-like and heavily sclerotized. The data on the horned larvae of *T. australis* and other North American species just mentioned have not been published, but were kindly placed at my disposal by Dr. G. W. Byers, Lawrence, Kansas (*in litt.*).

The larvae under consideration in which sclerotized tips or horns have developed in stead of fleshy lobes thus live in terrestrial not saturated substrates where they do not ordinarily need support from a water surface film, and though a number of larvae living e. g. in unsaturated forest soil or wood have lobes and not horns, the possibility is obvious that there may be a correlation between sclerification of lobes into horns and susceptibility of biotope to desiccation or at least more terrestrial not saturated substrates.

It should be noted, however, that the larva of *T. juncea* when placed in water lifts the spiracular disc to the surface after some time.

Apart from *T. (Vestiplex) scripta* and *T. (Odonatisca) juncea*, all the other 9 above-mentioned known species with 2 or 4 more or less sclerotized horns are of the subgenus *Lunatipula*, and as mentioned *T. livida*, *T. lesnei* and *T. recticornis* are of the *T. livida*-group. It seems possible that the occurrence of such appendages is primarily characteristic of certain taxonomic groups (constitutional preadaptation, cf. Huxley, 1945, p. 449 seq.), secondarily serving as selected adaptations. It would be interesting to know whether also in other species of the *T. juncea*-group (subgenus *Odonatisca* Savchenko 1954) and of the *T. livida*-group (within the subgenus *Luna-*

*tipula*), all 4 dorsal and lateral spiracular lobes are sclerotized horns.

The idea that sclerotization of the lobes of the spiracular disc into horns is associated with lower degrees of humidity of the larval substrates such as non-saturation or susceptibility to desiccation, is supported by the wide variation in the size, shape, pigmentation and sclerotization of the lobes within the *Tipulinae*; for this variation is fairly closely correlated with the nature of the larval environment (Savchenko, 1954; Chiswell, 1956). Thus, according to Chiswell (1956, p. 411) "as a general rule, the lobes of aquatic or semi-aquatic species (those which live in saturated or very wet soil and moss) are all moderately long with flattened posterior surfaces, whereas in more terrestrial species (those which live in moist but not saturated soil or in decaying wood) the dorsal and ventral lobes are considerably shorter than the lateral ones and, although the ventral lobes are usually flattened, the dorsal and lateral lobes are conical. In some of the species that tunnel in decaying wood, the lobes of the disc are not shorter than those of many soil-living forms, but in others all the lobes are very short. In the aquatic and semiaquatic species there is usually a brown or pale brown stripe on one or both margins of each lobe, with darker patches at the base and tip of each ventral lobe. The more terrestrial species show a greater variation in the sizes, shape, and position of the pigmented areas, which are often heavily sclerotized and dark brown or black."

Theowald (1957, p. 205) does not deny the correlation in question, but illustrates with examples that it must not be too categorically asserted. Excepting larvae with long, hairy lobes which are known to him only from water, Theowald considers it unjustified to ascribe a function to the structure of the lobes, which may merely indicate in which environments the larvae preferably develop.

At the same time there is a considerable reduction in the length of the anal papillae in the more terrestrial species (Savchenko, 1954; Chiswell, 1956, p. 413; Brindle, 1957). In accordance with this at least all the known palaeartic, presumably also the known nearctic, tipuline larvae with 2 or 4 horny lobes including *T. juncea* (figs. 1, 3, 4, and 7) have short anal papillae.

Theowald (1957, p. 206) calls attention to the possibility that the anal papillae may be salt (chloride) absorbing organs of osmoregulation as in *Culicidae* and *Tendipedidae* (= *Chironomidae*) rather than gills, but gives examples to show that the correlation between development of these structures and humidity of the substrate is not absolute.

Considering all the evidence here discussed, there seems actually to be much to suggest that the sclerotization of the dorsal and lateral lobes of the spiracular disc as also the shortness of the anal papillae in the last instar larva of *T. juncea* are in some way ascribable to the non-saturation and susceptibility to desiccation of its sandy biotope. The absence of a water surface film explains why the lobes are not flat, soft and provided with marginal hairs as in aquatic and semi-aquatic species. The possibility that the sclerification of the lobes may be a more direct adaptation to dryness is a different problem.

While it may seem likely *a priori* that a certain degree of impermeability to water may be conferred by sclerotization (cf. also Kalmus, 1941; Lafon, 1943), there are actually also instances of soft-skinned insects being resistant to desiccation (clothes moth larvae according to Mellanby, 1934), and a superficial layer of grease or wax rather than sclerification is known to be responsible for the impermeability to water in the cuticle of many insects (cf. Wigglesworth, 1950, p. 27—28; Richards, 1951, p. 299 seq.; Edney, 1957, p. 10 seq.).

To this comes that the surface of the spiracular lobes is only a very small fraction of the body surface. It seems that any impermeability conferred to them by sclerotization cannot contribute materially to the water economy of the larva. It would perhaps be worth while considering the possibility that not only the anal papillae but also the spiracular lobes may have some function, osmoregulatory or otherwise, correlated with the degree of humidity of the substrate independently of water permeability.

Among known European tipulid larvae those of *T. livida* and possibly of *T. recticornis* are the only ones which like that of *T. juncea* have both the dorsal and the lateral spiracular lobes sclerotized into horns. In all three species the dark horns are anteriorly curved, but in *T. livida* and the presumed *T. recticornis* the lateral ones are curved downwards; in *T. juncea*, upwards. In *T. livida* and the presumed *T. recticornis* the bases of the anterior horns do not reach down between the two spiracles, whereas in *T. juncea* they do. These bases are sclerotized in *T. livida* and *T. juncea* but not in the presumed *T. recticornis*. The tiny ventral lobes are fleshy in *T. livida* and the presumed *T. recticornis*, black and sclerotized in *T. juncea*. The Canarian *T. lesnei*, which has black horns, is like the other two *Lumatipula* species, *T. livida* and the presumed *T. recticornis*, as regards the characters above mentioned as common to these two species, except that its ventral lobes are provided with a dark spot on their upper surface. The head capsule of *T. juncea* as pictured in fig. 5 differs distinctly from that of *T. livida* as pictured by Chiswell (1955).

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### Summary.

Three stages of larvae reared from eggs of *Tipula juncea* Meigen and a full-grown larva and a pupa found in nature, and which are no doubt of the same species, are pictured and discussed as well as head capsules and spiracular discs of various stages. As in *Tipula (Lunatipula) livida* v. d. Wulp, *Tipula (Lunatipula) lesnei* Pierre and presumably *Tipula (Lunatipula) recticornis* Schumel, the dorsal and lateral lobes of the spiracular disc of the 4th instar larva of *T. juncea* are heavily sclerotized as long anteriorly curved horns. Reasons are given for believing this to be correlated with the relative dryness of its sandy biotopes.

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