PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Pleistocene Helophorus (Coleoptera, Hydrophilidae) from Borislav and Starunia in the Western Ukraine, with a Reinterpretation of M. Lomnicki's Species, Description of a New Siberian Species, and Comparison with British Weichselian Faunas

R. B. Angus

Phil. Trans. R. Soc. Lond. B 1973 **265**, 299-326
doi: 10.1098/rstb.1973.0030

PLEISTOCENE *HELOPHORUS* (COLEOPTERA, HYDROPHILIDAE) FROM BORISLAV AND STARUNIA IN THE WESTERN UKRAINE, WITH A REINTERPRETATION OF M. ŁOMNICKI'S SPECIES, DESCRIPTION OF A NEW SIBERIAN SPECIES, AND COMPARISON WITH BRITISH WEICHSELIAN FAUNAS

By R. B. ANGUS
Hope Department of Entomology, University of Oxford†

(*Communicated by J. W. S. Pringle, F.R.S. – Received* 3 *July* 1972)

[Plates 35 and 36]

CONTENTS

The five *Helophorus* species described by Łomnicki (1894) from fossils in oil-impregnated Pleistocene silts at Borislav, near Lvov, are redescribed and indentified as modern species. Four of Łomnicki's names fall into synonymy, but the fifth, *H. praenanus*, replaces *H. jacutus* Poppius for an eastern Siberian species.

The fossil *Helophorus* collected along with the Woolly Rhinoceros by the University of Krakow expedition to Starunia in 1929 are identified, and nine species, all still extant, are present in the sample.

---

† Present address: Department of Geology, The University of Birmingham.

These include four species which today live over much of Europe, two which are exclusively eastern Siberian, one found in both eastern Siberia and arctic North America, and two which are widely distributed over Siberia and extend into northern Europe and North America. It is concluded that the climate at Starunia during the period when the deposit was laid down was colder and more continental than at present, but it is stressed that since the assemblage of species found as fossils at Starunia does not exist in any one place today, there may be no exact modern climatic equivalent to Pleistocene Starunia.

The Starunia *Helophorus* fauna is compared with the Orthoptera as described by Zeuner (1934). In both cases there is a mixture of European and Siberian species, but the Orthoptera differ from the *Helophorus* in including a number of montane species. Neither group contains any species today found only in the high arctic.

The Starunia deposit has been ^{14}C dated at about 23000 years B.P., and its fauna is compared with British faunas from the same general period of the last glaciation. The faunas are broadly similar, but the Starunia fauna shows evidence of greater dampness perhaps associated with the period of maximum Weichselian glacierization.

The Siberian *Helophorus* formerly included in *H. brevipalpis* Bedel, present in both the Starunia sample and British deposits, is shown to be a distinct species, and is described as *H. aspericollis*, sp.nov.

1. INTRODUCTION

Although the occurrence of fossil insects in Pleistocene deposits has long been recognized, it is only recently, largely as a result of the work of G. R. Coope and his colleagues at the University of Birmingham, that it has been realized that most, if not all, of the species represented are still extant, though many now inhabit areas far removed from the fossil sites. Study of Pleistocene fossil assemblages thus shows changes in insect distribution, which may be used in investigating past climates, and in attempts to trace the histories of present-day faunas. This work is reviewed by Coope (1970).

As mentioned by Coope (1970, pp. 99–100), most of the identifiable fossils are the remains of various Coleoptera, and most of these consist of isolated heads, prothoraces and elytra and, more rarely, abdomens. On the basis of this material it has been possible to draw up quite a long list of *Helophorus* species occurring in Britain at various times during the Ice Age, but many fragments remain unidentifiable, and the identification of some species, such as *H. orientalis* Motsch., is always difficult (Angus 1970*a*).

Clearly it would be of enormous value to find a site at which the fossils were better preserved, and in particular, one in which more or less complete specimens occurred. Such a site would not only allow a more detailed investigation of its own fauna than is possible on fragments, but, by showing certain species to be definitely present in Pleistocene deposits, could give added confidence to identifications based on fragments. (It should at this stage be pointed out that many reliable identifications are possible on the basis of fragments, even in *Helophorus*, but the smaller species of this genus are particularly difficult to separate.)

In the eastern Carpathians, south of Lvov, are deposits of Miocene silt, which contain both salts (mainly sodium chloride) and heavy bituminous oil, forming a mineral termed 'ozocerite' by Nowak & Panow (1930). These silts are overlain by Pleistocene deposits into which the ozocerite has permeated, and in the course of mining the oil-shales many well-preserved fossils have been noted (Łomnicki 1894, 1914*a*). At one site, Borislav (Borysław in Polish), southeast of Lvov, Łomnicki (1894) recorded an extensive beetle fauna, with some northern and eastern (Siberian) species, and some which he described as new, including five *Helophorus*. At a second site, Starunia, south of Lvov, the remains, including soft parts, of Woolly Rhinoceros (*Coelodonta antiquitatis* Blum.) and Mammoth (*Elephas primigenius* Blum.) were found, but Łomnicki (1914*b*) and Raciborski (1914) found that all the insect and plant remains belonged to species living in the area at the present time. This was later explained as a result of an expedition to Starunia by a party from the University of Krakow in 1929, when it was found that shafts dug in earlier mining operations had been filled in with material thrown down from the surface, and in the excavations of 1907 these infillings had been confused with the surrounding Pleistocene silts (Nowak & Panow 1930, suppl. 4). This expedition, which found a second Woolly Rhinoceros, also collected insect remains, including *Helophorus*, from undoubted Pleistocene deposits.

2. THE BORISLAV *HELOPHORUS*

As mentioned above, the fossil *Helophorus* from Borislav were described by Łomnicki (1894). He placed them in five species, *H. pleistocenicus* (of which a var. *obsoletus* was described), *dzieduszyckii*, *kuwerti*, *praenanus* and *polonicus*, all described as new. In the course of 10 months work in the Soviet Union, under the exchange sponsored by the Royal Society and the Soviet Academy of Sciences, I was able to visit Lvov, where Łomnicki's collection is kept, and found that these five species are in fact all modern ones (four in all), as follows: *H. pleistocenicus* Łom. = *sibiricus* Motsch.; *H. pleistocenicus* var. *obsoletus* Łom. & *H. dzieduszyckii* Łom. = *aquaticus* (L.); *H. kuwerti* Łom. = *oblongus* LeConte; while *H. praenanus* Łom., with *polonicus* Łom. as a synonym, becomes the valid name for *H. jacutus* Poppius, 1907.

The specimens are mounted on cards, and are often embedded in small blocks of silt. As both the beetle fragments and the silt are slightly waxy with ozocerite, the glue does not hold them very firmly to the cards, and some of the specimens have been lost. In some cases, as indicated below, specimens are more or less intact, and it has been possible to extract aedeagophores from specimens of three of the four species. In Lvov I mounted the aedeagophores in aqueous D.M.H.F. resin (see Angus 1970*b*, p. 5), but as a result of work in Oxford on the Starunia fossils, found that the preparations clear better if treated with alcohol and benzene, and mounted in Canada Balsam. I therefore remounted all the Lvov preparations except the *H. praenanus* aedeagophore, which was too delicate.

The fossils all bear printed labels 'Borysław insec. fossil', and some also have Łomnicki's handwritten name labels. I have designated lectotypes and paralectotypes, and have labelled all the specimens accordingly.

In addition to the material in Łomnicki's collection there are some specimens in d'Orchymont's collection in Brussels. These have the same printed data labels as those in Łomnicki's collection, and various handwritten labels, as described under the relevant species.

One of the most striking features of all the fossils is their extreme darkness of colour, in many cases amounting to total – sometimes even metallic – blackness, even on the legs, which are very rarely black in *Helophorus*. I am sure that this is a result of the fossilization, probably being associated with the black pitchy ozocerite. However, although prolonged immersion of a paralectotype of *H. kuwerti* from d'Orchymont's collection, in benzene, removed some black oil, there was no lightening of colour. Immersion of the Starunia fossils in benzene released copious amounts of oil, and left normal light coloured beetles. This will be further discussed when the ages of the fossils are considered (p. 312).

(*a*) *H. sibiricus* (Motsch.)

Empleurus sibiricus (Motschulsky 1860, p. 104).
H. sibiricus (Angus 1970*b*, p. 16).
H. (*Trichelophorus*) *pleistocenicus* (Łomnicki 1894, p. 65; plate VI, figure 52).

Łomnicki's material of *H. pleistocenicus* comprises two species, *H. sibiricus* and *H. aquaticus*. Although there is an *H. aquaticus* elytron in d'Orchymont's collection, labelled by Łomnicki as *H. pleistocenicus* var. *obsoletus*, none of the Lvov material is labelled as *obsoletus*, and the two species were mingled in the series. Thus only the labelled specimen is recognizable as representing *obsoletus*.

The material is as follows:

H. sibiricus. One head, thorax, elytra and bits of leg, here designated **lectotype**; 4 × head, thorax and elytra; 13 pairs of elytra; 5 × right elytron + abdomen, one dissected to give aedeagophore; one left elytron + abdomen; forty-four left elytra and thirty-nine right elytra. These are all paralectotypes and in addition to my handwritten labels bear blue printed 'paralectotype' labels.

H. aquaticus. Two pairs of elytra + abdomen; 23 left elytra, 27 right elytra and one elytral fragment. These specimens are also paralectotypes of *H. pleistocenicus*, but are without value in identifying that species. They bear my handwritten labels, but no printed ones. Some or all of these specimens may have been classed by Łomnicki as var. *obsoletus*, but there is no way of knowing this.

In addition to the material in Łomnicki's collection, there are additional specimens in the d'Orchymont collection, as follows:

(1) The holotype of *H. lomnickii* d'Orchymont, discussed by Angus (1970*b*). This is shown by its labels to be a further paralectotype of *H. pleistocenicus*, and it is also *H. sibiricus*. In my 1970*b* paper I stated that this specimen was also labelled '*T. lomnicki* Reg. ex typis', but it is now clear from study of other Łomnicki specimens in the d'Orchymont collection that this label is in fact '*J. Łomnicki* Leg. ex typis', indicating that d'Orchymont received the material from J. Łomnicki (M. Łomnicki's son), and that Regimbart is not involved.

(2) A head and prothorax of *H. sibiricus* labelled as '*Trichelophorus pleistocenicus* M. Łom.'. This is a further paralectotype.

(3) A right elytron of *H. aquaticus* labelled '*Trichelophorus pleistocenicus* M. Łom. var. *obsoletus* M. Łom.'. This is here designated **lectotype** of *H. pleistocenicus* var. *obsoletus*.

Lectotype. *Helophorus pleistocenicus* Łomnicki. – *Length*: about 5.8 mm; *breadth*: 2.6–2.7 mm. (The approximations allow for distortion.) *Head*: pitchy brown with reddish and greenish bronze reflexions; strongly, coarsely and evenly granulate throughout, surface of granules rough; stem of Y groove narrow linear. Antennae and palpi missing. *Pronotum*: slightly distorted, but of typical low-arched *H. sibiricus* pattern, widest a third of the way from the front, sides curved to a quarter of the way from the hind angles, then sinuate. All intervals closely and very strongly granulate, the granules rough, with distinct median pits. Grooves deep (? artefact), fairly narrow; median straight, tapered anteriorly; submedians curved outwards over their middle half, then sinuate either end; submarginals more or less straight, not reaching to either margin of the pronotum; marginals widened before the middle, as a result of the outward curve of the pronotal margins, with isolated granules on their floors. Suprapleural areas wide in anterior half, tapered posteriorly. (For nomenclature of pronotal grooves and intervals, see

Balfour-Browne 1958, p. 91). *Elytra*: crumpled, dull mid-brown; strongly striate, interstices 2, 4 and 6 raised in knife-like ridges, 7 and 8 more weakly raised. Flanks large, broader than epipleurs. Intercalary striae well developed, running into the suturals about a quarter of the way from their bases. The dark sutural ʌ mark is visible as a spot on the suture, about half way down, with paired spots on interstices 2 and 4 making up the rest of the ʌ. There are also paired spots on interstice 6, opposite the apex of the ʌ. The elytral apices are tapered. *Underside*: abdomen missing, metasternum and hind femora black. The rest of the underside is embedded in silt.

This specimen agrees with modern *H. sibiricus* in all its features except the rather dark colour. This appears to be a result of fossilization as all the specimens are unusually dark. The aedeagophore of a dissected paralectotype (which is completely black) is shown in figure 14, plate 35, while figure 13 shows the aedeagophore of a modern Finnish specimen.

All the *H. sibiricus* paralectotypes of *H. pleistocenicus* agree with the lectotype in the features preserved in them. The *H. aquaticus* paralectotypes of *pleistocenicus*, and *H. pleistocenicus* var. *obsoletus*, are discussed under *H. aquaticus*, after *H. dzieduszyckii*.

(*b*) *H. aquaticus* (L.) (*dzieduszyckii* Łomnicki)

Silpha aquatica (Linnaeus 1758, p. 362).
H. (*Meghelophorus*) *aquaticus* (Angus 1970*b*, p. 27).
H. (*Praehelophorus*) *dzieduszyckii* (Łomnicki 1894, p. 67; plate VI, figure 53)
H. (*Trichelophorus*) *pleistocenicus* var. *obsoletus* (Łomnicki 1894, p. 67).

As explained by Angus (1970*b*), *H. aquaticus* is the species previously known as *aequalis* Thomson. The larger European *Meghelophorus* is *H. grandis* Ill.

Łomnicki's material of *H. dzieduszyckii* consists of one head, thorax and elytra, here designated **lectotype**; and 5 left elytra and 2 right elytra, which are paralectotypes. The lectotype is labelled '*Praehelophorus dzieduszyckii* M. Łom.'. In d'Orchymont's collection there is a left elytron labelled '*Praehelophorus dzieduszyckii* M. Łom.'. This is a further paralectotype.

Lectotype. *H. dzieduszyckii* Łomnicki. – *Length*: about 5.5 mm; *breadth*: about 2.2 mm. *Head*: shining blackish pitchy with gold and maroon reflexions; stem of Y groove rather widely expanded anteriorly; central area of head, in front of the fork of the Y groove, punctate, shining between the punctures, though there are some impressed rings and other irregularities. The rest of the head is granulate, but still shining. Antennae and palpi missing, except for the scape of the left antenna, which is dark brown. *Pronotum*: moderately arched, flattened over the internal intervals; widest a third of the way from the anterior margin, sides evenly curved to a sixth of the way from the hind angles, then sinuate. Ground colour pitchy black with red and golden bronze reflexions. Grooves distinct, moderately deep, even; median groove straight, widest in middle, evenly tapered to ends; submedians sharply angled outwards medially, and equally sharply sinuate a quarter of the way from each end; submarginals straight, parallel to median, slightly wider than the other grooves and very slightly tapered to ends; marginals indistinct, shallow, granulate as external intervals; raised margins narrow, crenulate, distinct to hind angles. Internal intervals shining, finely and closely punctate, with some impressed rings round the punctures; middle intervals with fine flattened very shining granulation; externals coarsely granulate, the granules rough, but still shining. *Elytra*: dark brown, with the dark sutural ʌ mark and paired spots on interstice 6 just discernible. Rather strongly striate; intercalary striae well developed, the left one of 8 or 9 punctures, and running into the sutural stria, diverting it so that its basal 10 punctures are isolated from the rest of the stria; right intercalary stria of 9 punctures, confluent with, but not diverting, sutural stria. Elytral flanks narrow; all interstices evenly raised.

This specimen is identified as *H. aquaticus* by the reduction of the granulation towards the centre of the pronotum, and the even ridging of the elytral interstices. The paralectotype elytra have the striae of varying strength, both finer and coarser than the lectotype. The intercalary striae are of 5, 4 or 3 (larger) punctures. None of the specimens shows any uneven ridging of the alternate interstices, which would be suggestive of *H. grandis*.

It will be noted that Łomnicki erected the subgenus *Praehelophorus* for *H. dzieduszyckii*: this is therefore synonymous with *Meghelophorus* Kuwert 1866.

The *H. aquaticus* included among the paralectotypes of *H. pleistocenicus* have a similar appearance to the *dzieduszyckii*. One has the complex pale elytral markings characteristic of Sharp's var. *splendens*. The seventh sternite of one of the two abdomens (♀) is shown in figure 8, plate 35, and may be seen to have similar fine teeth to the modern specimen shown in figure 7.

The lectotype of *H. pleistocenicus* var. *obsoletus* (a right elytron) is 4.3 mm long and 1.3 mm broad. The striae are fine and the interstices evenly raised. The ground colour is uniform dark brown, with the ʌ mark (half of it) and the spot on interstice 6 just visible. The flank is narrow.

None of the specimens shows any tendency towards the uneven ridging of the elytral interstices characteristic of *H. grandis*, and there is no reason to suspect that this species is present among the material.

(*c*) *H. oblongus* LeConte (*kuwerti* Łomnicki)

H. oblongus (LeConte 1850, p. 217; Angus 1970*c*, p. 261).
H. kuwerti (Łomnicki 1894, p. 73; plate VI, figure 56).

Angus (1970*c*) gives an account of *H. oblongus*, and synonymizes the eastern Siberian *H. laevicollis* Poppius with it.

Łomnicki's material of *H. kuwerti* is as follows: 1 more or less complete specimen, a male whose aedeagophore I have extracted, here designated **lectotype**; 2 × head, thorax and elytra; 1 prothorax; 1 pair of elytra; 1 left elytron and 1 very broken right elytron. These are all paralectotypes. There is also a card point from which the specimen has been lost. The lectotype is labelled in German as having been compared with *H. niger*, *sibiricus*, etc. One of the more complete paralectotypes has a red pencilled '*kuwerti* M. Łom.' label.

The d'Orchymont collection contains a further paralectotype, a head, prothorax and elytra, and some bits of leg, all dissociated but mounted together on the same card. These were presumably removed by d'Orchymont from a small piece of silt. This specimen is labelled '*Helophorus kuwerti* M. Łom.' and 'J. Łomnicki leg. ex typis.'.

Lectotype ♂. *H. kuwerti* Łomnicki. – *Aedeagophore*: figure 16, plate 35. (To be compared with the aedeagophore of modern Siberian *H. oblongus*, figure 15.) *Length*: about 5.5 mm; *breadth*: about 2.3 mm. *Head*: shining black, sparsely punctate, becoming rugose by eyes; stem of Y groove narrow linear; sides of clypeus bordered by a distinct narrow groove, outside of which is a raised margin; maxillary palpi (one is present, detached) shining black, apical segment asymmetrically pyriform; antennae (the right one is present, folded under the eye) dark brown, 8-segmented. *Pronotum*: shining black, weakly but evenly arched; anterior corners folded down (artefact!); grooves narrow, shallow; median straight, tapered at ends; submedians weakly curved outwards at middle, sinuate a quarter of the way from each end; submarginals parallel to median; marginals narrow, even, distinct to hind angles, bordered by narrow raised margins.

Pronotal intervals sparsely and very finely punctate. *Elytra*: shining black, rather weakly striate; no intercalary striae present; interstices wide and flat; flanks narrow; *Legs*: most of the femora are present (detached), plus the tibiae and tarsi of the right front and middle legs. They are all shining black, rather elongate. *Abdomen*: black.

The two more or less intact paralectotypes are very similar to the lectotype. One is slightly larger and has the pronotum with slight greenish pitchy reflexions. The paralectotype in d'Orchymont's collection is shown in figure 2, plate 35, while figure 1 shows a modern Siberian specimen for comparison.

H. oblongus is a very distinctive species, easily recognizable by its large size (length 4.5–6.5 mm), 8-segmented antennae, form and sculpture of the head and pronotum, absence of intercalary striae, and aedeagophore. All these features are shown very clearly by the fossils, although the fossil aedeagophore (figure 16, plate 35) is not cleared as it was photographed in D.M.H.F. (The parts disarticulated when I transferred it to Canada Balsam.) Nevertheless, it may be seen that the size, shape of the parameres, and length of the aedeagal struts all agree with the Siberian specimen shown in figure 15, plate 35. The distinct groove and ridge at the sides of the clypeus are useful in distinguishing isolated heads from those of *H.* (*Meghelophorus*) *niger* J. Sahlb., which are otherwise similar in size and sculpture.

Modern *H. oblongus* may have the elytra either mid brown with dark marks on the suture and sixth interstice, or they may have uniform dark brown elytra. In the fossils there is certainly some *post mortem* darkening, as shown by the legs, which are brown or reddish in modern specimens. In the d'Orchymont specimen the dark mark on the sixth elytral interstice is discernible, appearing more distinct than in the darkest modern specimens. It is thus not possible to say what the original colour of the Borislav specimens was.

(*d*) *H. praenanus* Łomnicki (*polonicus* Łomnicki, *jacutus* Popp., *birulai* Zaitzev)

H. praenanus (Łomnicki 1894, p. 69; plate VI, figure 54).
H. polonicus (Łomnicki 1894, p. 71; plate VI, figure 55).
H. jacutus (Poppius 1907, p. 7; Angus 1970*c*, p. 278).
H. birulai (Zaitzev 1910, p. 48).

Angus (1970*c*) gives an account of *H. jacutus*, in which its occurrence as a Pleistocene fossil is mentioned. It is now necessary to replace the name *jacutus* with the older *praenanus* Łomnicki, and the opportunity is also taken of adding *H. birulai* Zaitzev to the synonymy.

H. praenanus Łomnicki. – Łomnicki's material of *H. praenanus* is as follows: 1 head, thorax, elytra and bits of leg, embedded in a block of silt. This specimen is labelled '*Helophorus praenanus* M. Łom.' and is here designated **lectotype**. The abdomen, if present, is deeply embedded in the silt, and no attempt has been made to dissect it. The paralectotypes are as follows: 1 pair of elytra with meso- and metathorax and abdomen, dissected and aedeagophore extracted; 1 head, thorax and elytra; 1 prothorax and elytra, disarticulated but embedded together in a piece of silt; 1 pair of elytra; 1 pair of soft elytra with abdomen; 7 left elytra; 1 right elytron with bits of underside embedded in silt; 1 left elytron with abdomen, possibly ♀ as no aedeagophore was found on dissection; 5 right elytra. There are also three cards from which the specimens have been lost.

D'Orchymont's collection contains a right elytron labelled '*Helophorus praenanus* M Łom.' and 'J. Łomnicki leg. ex typis'. This is also a paralectotype.

Lectotype. *H. praenanus* Łomnicki. – *Length*: about 3.7 mm; *breadth*: about 1.5 mm. *Head*:

shining black-bronze with greenish reflexions; punctate, with slight irregularities between the punctures near the hind margin; stem of Y groove narrow but expanded anteriorly; antennae and palpi missing, except scape of left antenna which is brownish. *Pronotum*: shining blackish bronze, as head; anterior margin narrowly reddish brown. Moderately and rather evenly arched, widest a little before the middle, sides evenly curved to base. Grooves narrow, distinct; median straight, tapered at extreme ends; submedians bluntly angled outwards medially (no rounding of angle), sinuate a fifth of the way from the hind angles; submarginals straight, weakly divergent anteriorly, so that the middle intervals are a little wider in front than behind; marginals narrow, distinct to hind angles. Internal and middle intervals with sparse fine punctures, the anterior quarter of the middle intervals with slight unevenness between these punctures. External intervals with similar punctures and very weak smooth granules round them. *Elytra*: a little crumpled. Mid-brown with the darker sutural ʌ mark visible. Moderately striate (no intercalaries). Flanks not visible from below. *Legs*: apparently fairly elongate; same colour as elytra; no tarsi visible.

The paralectotypes are much as the lectotype, but the head, prothorax and elytra specimen is very dark. The elytra of the dissected male, whose aedeagophore is shown in figure 27, plate 36, are very similar to those of the lectotype.

These specimens, apart from their generally darker colour (see above, p. 301), agree with modern *H. jacutus* in all respects. The paralectotype aedeagophore shown in figure 27 is disarticulated and lacks the basal piece, but the size and shape of the parameres (figure 27*b*), and of the tube and struts, including the relative length of the struts (figure 27*a*), are seen to be in complete agreement with those of a modern Siberian specimen (the lectotype of *H. jacutus* Poppius, figure 29), and with a well-preserved fossil from Starunia (figure 28). There can thus be no doubt that *H. praenanus* is conspecific with modern Siberian *jacutus*, so the use of the older name becomes necessary.

H. polonicus Łomnicki. – Łomnicki's material of *H. polonicus* is as follows: 1 head, thorax, elytra, abdomen and bits of leg, here designated **lectotype**; 1 left elytron and 1 right elytron, both paralectotypes. The lectotype is labelled '*polonicus* M. Łom.' It is female.

Lectotype ♀. *H. polonicus* Łomnicki. – *Length*: about 4 mm; *breadth*: about 1.5 mm *Head*: shining black, punctate as in the *H. praenanus* lectotype, except that the punctures are a little closer and the ground colour is less shining. The anterior part of the stem of the Y groove is widened, but most of the stem is concealed under the front of the pronotum. Antennae and palpi missing. *Pronotum*: shining black, anterior margin yellowish brown. Distorted through flattening, and folded down at the anterior corners. Configuration of grooves as in the *praenanus* lectotype. The fine puncturation of the internal and middle intervals is closer than in the *praenanus* lectotype and the granulation of the externals is distinct, much stronger than in the *praenanus* lectotype, though still shining. The sides are rounded to the base and the marginal grooves are distinct to the hind angles. *Elytra*: right one overlapping left. Mid-brown with the dark sutural ʌ mark indistinct. Striae weak and narrow. Flanks narrow.

This specimen is a female *praenanus*. The slight differences in sculpture between it and the lectotype of *praenanus* fall well within the range of variation of modern Siberian specimens, as well as British Pleistocene fossils. The paralectotypes also show no features untypical of *praenanus*, though it should be pointed out that identification of isolated elytra of the smaller *Helophorus* species is not normally possible.

H. birulai Zaitzev. – Zaitzev described *H. birulai* from a single specimen taken by von Toll near Zhigansk (Shigansk in Poppius' writings) on the River Lena in eastern Siberia. This specimen is in Zaitzev's collection in the Zoological Institute, Leningrad. It is labelled '**Окр. Жиганск на Лене. Толь.** VI–VII.03' (near Zhigansk on the Lena. Toll. vi–vii. 03), '*Heloph. birulai* m. spec. typ. ii.08. Zaitzev det.' and '= *jacutus* Popp. sp. *immaturum*! (ix. 1942)'. Thus Zaitzev himself came to realize that his *H. birulai* was not a distinct species.

Holotype ♀. *H. birulai* Zaitzev. – *Length*: 3.5 mm; *breadth*: 1.7 mm. *Head*: dark shining greenish pitchy with bronze reflexions; shining, rugosely punctate, becoming granulate anteriorly and near eyes; stem of Y groove moderately expanded anteriorly. Maxillary palpi dull yellow, short, apical segment strongly asymmetrical. Antennae dull yellow, 9-segmented. *Pronotum*: moderately arched, but flat longitudinally; widest a little before middle, sides evenly curved to base. Ground colour pitchy greenish, anterior margin dull yellow. Grooves narrow, fairly deep; median straight, tapering anteriorly; submedians curved outwards just behind middle, sinuate at ends; submarginals weakly curved outwards medially, slightly divergent anteriorly; marginals distinct to hind angles, almost as wide as the other grooves; narrow raised margins distinct. Internal and middle intervals smooth and shining, with sparse fine punctures, and some impressed rings round these, except in the middle section of the intervals; externals with weak low rounded granules. *Elytra*: dull greyish fawn, the sutural ʌ mark and spots on interstice 6 vaguely darker. Moderately striate, no intercalaries; striae narrow, interstices weakly convex. Flanks not visible from below. *Legs*: dull yellow, not very long: tarsi with weak swimming-hairs.

This is a soft female *H. praenanus*. It is a little unusual in the complete absence of any longitudinal arching (doming) of the pronotum, which is also rather transverse. However, even in these characters it falls within the range of variation of *H. praenanus*, and there is no reason why it should not be referred to that species.

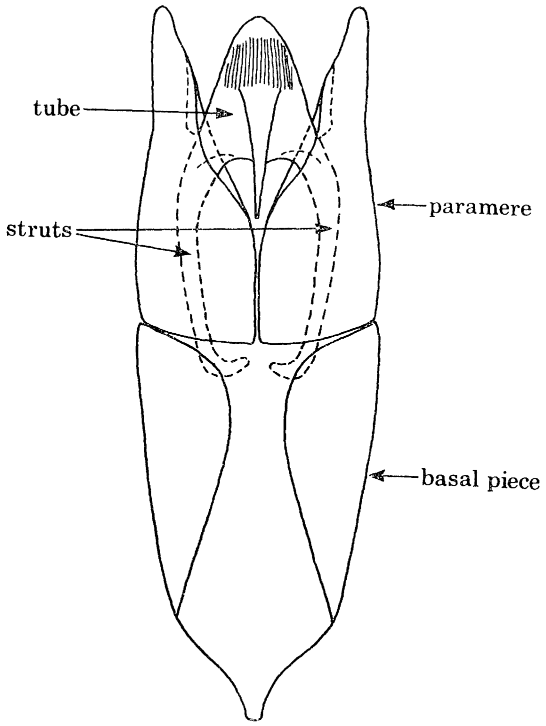


Figure 50. Aedeagophore of *Helophorus grandis* Ill., to show the structures mentioned in descriptions. The tube and struts together comprise the aedeagus.

3. The starunia *Helophorus*

Stach (1930, p. 21) mentions the presence of *Helophorus* among the insect remains taken in association with the second Woolly Rhinoceros at Starunia. These fossils were sent to me, in tubes of alcohol, by Dr J. Pawłowski of the Zoological Institute of the Polish Academy of Sciences, Krakow. I have worked through these and mounted many of the identifiable fragments on strips of card, of the type used by Dr Coope and his colleagues at Birmingham.

These card strips consist of pieces of Bristol Board the same size and shape as glass microscope slides. At each end of the strip is a piece of thick cardboard, over which a glass microscope slide is placed. This leaves the central portion of the card free for the mounting of fossils, which are protected by the glass slide. The card and slide are held in position, and further protected, by being placed in aluminium trays whose sides are folded upwards and just over the edges of the glass slides. The ends are clear, so that the card and slide may be slid in and out of the tray. The only trouble with this arrangement is that the height at which the sides of the aluminium trays are folded inwards is critical: if it is fractionally too high the card and slide are not held in place, and if it is too low they are gripped so tightly that when they are slid back after examination the card is liable to buckle under the slide, damaging the specimens. Nevertheless, these cards seem to be the most satisfactory way of storing dry insect fossils, which are normally too fragile to be left exposed on ordinary entomological cards or card points.

The fossils were heavily impregnated with thick oil, which was removed by soaking them in benzene. They are in general very well preserved, and where the abdomen is present it has been possible to dissect out the genitalia The aedeagophores were further cleared in benzene and mounted in Canada Balsam, on slides The card strips bearing the beetles are numbered (there are 10 of them), and the beetles are numbered along each card. It is thus possible to cross-refer the various genitalia preparations to their relevant specimens.

The fossils themselves consist of intact beetles (with legs, antennae and palpi variously present or not, but this is not stated when listing them), heads, prothoraces, heads and prothoraces together, pairs of elytra with the meso- and metathoraces (the pterothorax) and abdomens, isolated elytra, and 'compound fragments', which may be one or both elytra with bits of thorax and abdomen. I have only used this term for specimens left in alcohol.

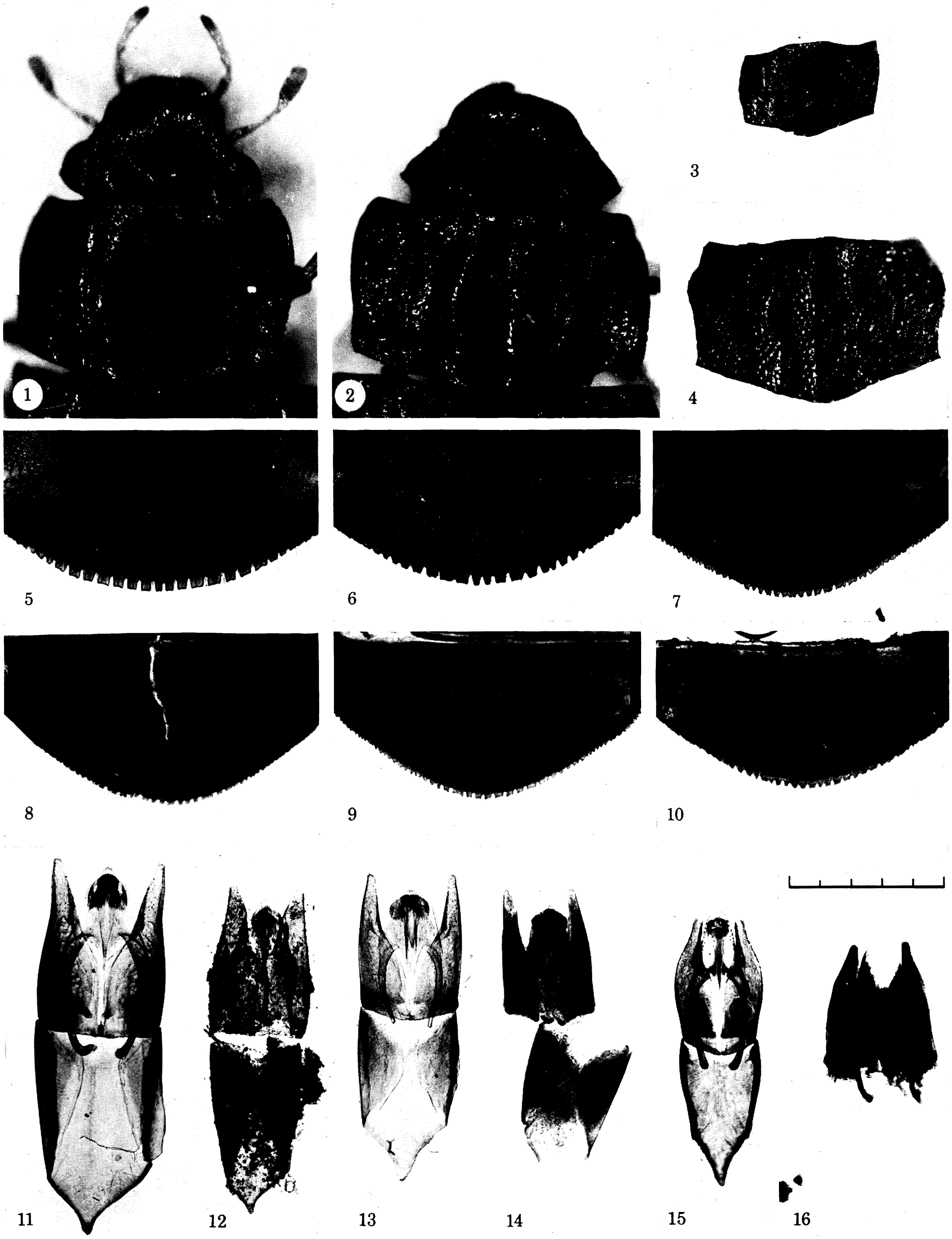
Description of plate 35

Figures 1–4. Heads and pronota of modern and fossil *Helophorus*. 1, Modern *H. oblongus* LeC. from Siberia, head and pronotum; 2, fossil *H. oblongus* from Borislav (a paralectotype of *H. kuwerti* Łom.), head and pronotum; 3, fossil *H. orientalis* Motsch. from Staurnia, pronotum; 4, fossil *H. grandis* Ill. from Starunia, pronotum.

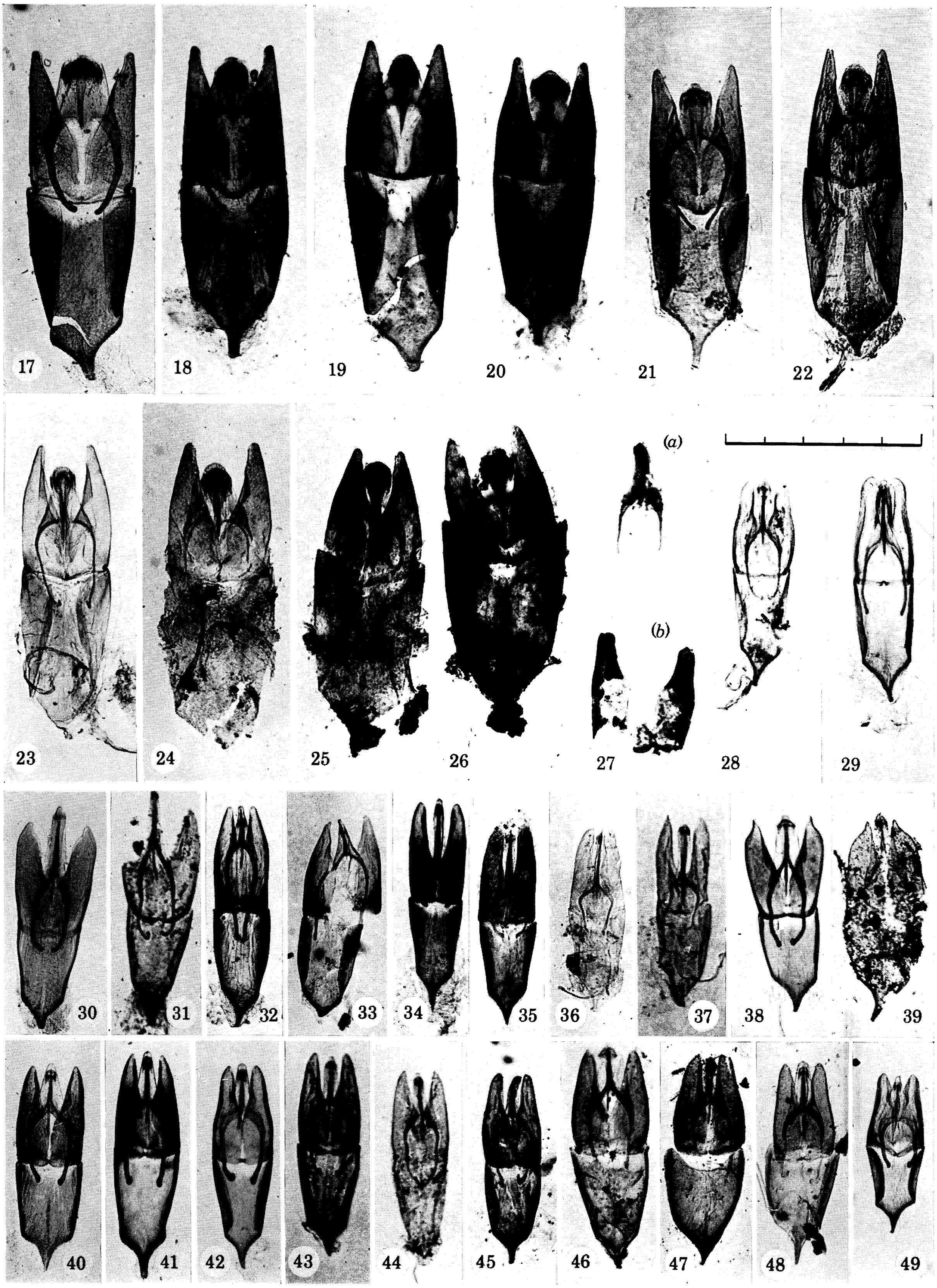
Figures 5–10. Seventh abdominal sternites of modern and fossil *Helophorus*. 5, *H. grandis* Ill., lectotype; 6, *H. grandis*, a fossil from Dorchester on Thames, Oxfordshire; 7, *H. aquaticus* (L.), a modern specimen from Scotland; 8, fossil *H. aquaticus* from Borislav (a paralectotype of *H. pleistocenicus* Łom., not conspecific with the lectotype); 9, fossil *H. aquaticus* from Starunia; 10, fossil *H. aquaticus* from Dorchester on Thames.

Figures 11–16. Aedeagophores of modern and fossil *Helophorus*. (For explanation of aedeagal parts see figure 50 (p. 307).) 11, *H. grandis* Ill., lectotype; 12, fossil *H. grandis* from Dorchester on Thames; 13, modern *H. sibiricus* Motsch., from Finland; 14, fossil *H. sibiricus* from Borislav (a paralectotype of *H. pleistocenicus* Łom.); 15, modern *H. oblongus* LeConte from Siberia (*H. laevicollis* Popp., lectotype); 16, fossil *H. oblongus* from Borislav (*H. kuwerti* Łom., lectotype).

The linear scale represents 1 mm for figures 1–4, 0.5 mm for figures 5–16.



FIGURES 1 TO 16. For legends see facing page



FIGURES 17 TO 49. For legends see facing page

The list of species, with the number and nature of the fragments, is as follows. Unless otherwise stated, the specimens are mounted on cards.

H. (*Gephelophorus*) *sibiricus* Motsch.	1 left elytron
H. (*Meghelophorus*) *aquaticus* (L.)	3 intact beetles; 1 head; 3 prothoraces; 5 heads and prothoraces; 15 pairs of elytra with pterothorax and abdomen. *In alcohol*: 46 compound fragments; 61 left elytra and 62 right elytra
H. (*M.*) *grandis* Ill.	1 head and prothorax
H. (*Atracthelophorus*) *glacialis* Villa	2 pairs of elytra with pterothorax and abdomen (♂♂)
H. (*A.*) *aspericollis* sp.nov.	4 intact beetles (2 ♂♂, 2 ♀♀); 9 pairs of elytra with pterothorax and abdomen (♂♂); 1 head and prothorax
H. (*s.*) *str. orientalis* Motsch.	1 intact beetle; 1 thorax, elytra and abdomen (♀♀)
H. praenanus Łomnicki	1 pair of elytra with pterothorax and abdomen (♂)
H. browni McCorkle	1 pair of elytra with pterothorax and abdomen (♂)
H. discrepans Rey	1 pair of elytra with pterothorax and abdomen (♂)
Unidentifiable	14 pairs of elytra with pterothorax and abdomen (12 ♀♀, 2 ♂♂ with only the basal piece of the aedeagophore present). *In alcohol*: 1 pair of elytra with mesothorax; 21 elytra

4. DESCRIPTION OF *H. ASPERICOLLIS* SP.NOV.

Helophorus* (*Atracthelophorus*) *aspericollis sp.nov.

H. aspericollis (Reitter, named in collection, but not published).
H. brevipalpis Bedel, *pars* (Angus 1970*c*, p. 255).
'Siberian style' *H. brevipalpis* (Coope 1970, p. 103).

The Siberian *Helophorus* species hitherto referred to *H. brevipalpis* Bedel differs from the European species in a number of characters, notably the distinctly larger aedeagophore with relatively longer struts, the more coarsely granulate pronotum and the more strongly striate elytra. These differences are slight (figure 51), and only the aedeagal character is absolutely reliable, though specimens in which both the pronotum and elytra are intermediate are very rare.

In view of the similarity of the two forms, and their different geographical distributions, it

---

DESCRIPTION OF PLATE 36

FIGURES 17–49. Aedeagophores of modern and fossil *Heloporus*. See figure 50 (p. 307) for explanation of parts. 17–20, Modern *H. aquaticus* (L.): 17, from Scotland; 18, 19, from Przemysl in S.E. Poland; 20, from Perm (Russia); 21–23, fossil *H. aquaticus* from Starunia; 24–26, fossil *H. aquaticus* from Dorchester on Thames; 27, *H. praenanus* Łom., paralectotype (a fossil from Borislav): *a*, tube and struts; *b*, parameres; 28, fossil *H. praenanus* from Starunia; 29, modern Siberian *H. praenanus* (*H. jacutus* Popp., lectotype); 30, *H. browni* McCorkle, holotype; 31, fossil *H. browni* from Starunia; 32, modern *H. discrepans* Rey (*H. iteratus* Sharp, lectotype); 33, fossil *H. discrepans* from Starunia; 34, modern Norwegian *H. glacialis* Villa; 35, fossil *H. glacialis* from Orleton, Herefordshire; 36, 37, fossil *H. glacialis* from Starunia; 38, *H. mongoliensis* Angus, holotype; 39, fossil *H. mongoliensis* from Dorchester on Thames; 40–42, *H. aspericollis* sp.nov., modern Siberian specimens: 40, holotype; 41, 42, paratypes from the Irkutsk oblast; 43–45, fossil *H. aspericollis* from Starunia; 46–48, fossil *H. aspericollis* from Dorchester on Thames; 49, modern *H. brevipalpis* Bed., from Oxfordshire.

The linear scale represents 0.5 mm.

might seem more reasonable to regard the Siberian population as a subspecies of *H. brevipalpis*, but a closer examination of the distributions of the two forms shows that this interpretation is not adequate. The distributions are shown on figure 57 (p. 318), and may be seen to be not only widely separated, but also in areas with very different climatic conditions. European *H. brevipalpis* has a distribution comparable with that of *H. aquaticus* (figure 53), while the distribution of the Siberian species appears broadly similar to that of *H. praenanus* (figure 58), with which it also occurs as a fossil in European Pleistocene deposits.

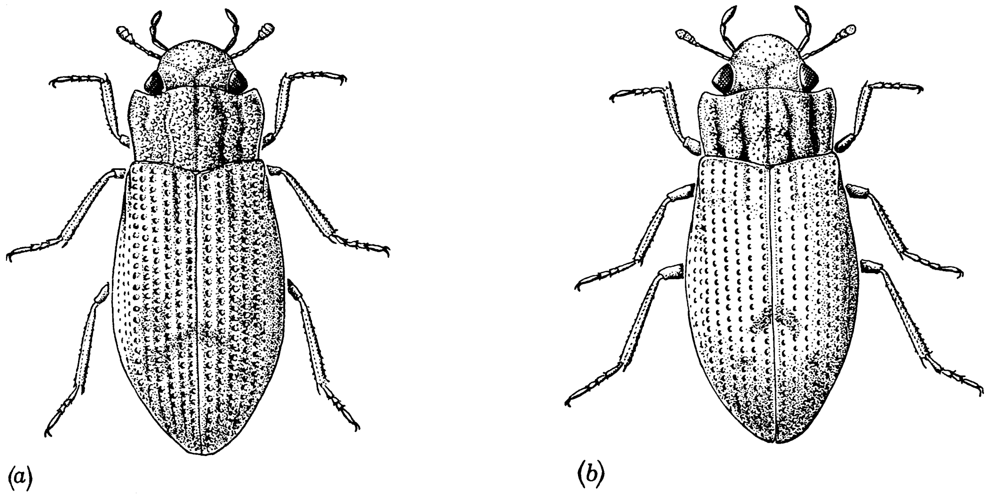


FIGURE 51. *Helophorus aspericollis* and *brevipalpis* (magn. × 23).
(*a*) *H. aspericollis* sp.nov., Holotype; (*b*) *H. brevipalpis* Bed., from Oxford.

It is thus necessary to describe the Siberian species as new, and the name chosen for it is *aspericollis*, as used by Reitter in his collection, because the most striking feature of these Siberian beetles is the very coarsely sculptured pronotum.

Helophorus aspericollis sp.nov. *Length*: 2.5–3.2 mm; *breadth*: 1.1–1.4 mm. *Aedeagophore*: figures 40–42, plate 36. *Head*: dark greenish or reddish bronze (sometimes black), rugosely granulate, the granules with median pits; sculpture occasionally reduced towards the fork of the Y groove; Y groove deep, its stem broadly expanded anteriorly. Antennae 9-segmented, pale brown, the clubs a little darker. Maxillary palpi yellowish to mid-brown, the apical segment a symmetrical oval, normally darker in its apical half. *Pronotum*: rather strongly arched, widest at the base of the anterior third, the sides curved to the hind angles, or occasionally straighter in the basal quarter. Anterior margin excised behind the eyes. Ground colour as head, with the anterior margin and marginal grooves dull yellow. All intervals normally strongly granulate, the granules with median pits. The sculpture is always a little weaker on the internal intervals, and is strongest on the externals, where there is no flattening of the tops of the granules. In some specimens the granules of the internal intervals may be low, rounded, smooth and shining, but this is not usual. Grooves distinct, fairly deep; median straight, sometimes widened medially, tapered to ends; submedians either angled or curved outwards medially, sinuate about a third of the way from each end (sometimes only weakly so anteriorly); submarginals normally curved outwards medially, but sometimes almost straight, slightly divergent anteriorly; marginals fairly wide and deep, distinct to hind angles, narrowed in anterior quarter. Lateral margins distinct, finely serrate. *Elytra*: dull yellow, sometimes grey or approaching mid-brown, with a dark sutural ʌ mark and darker spots on interstice 6. In some specimens there is an osbscure mottling over most of the elytral surface. Strongly striate, the interstices 1–1.5 times the width of the strial punctures, and the basal quarter of interstice two normally distinctly raised. Flanks broadly visible from below. *Legs:* dull yellow, rather short; tarsi with rather weak swimming-hairs; apical tarsal segment somewhat darkened, mid-brown in some specimens.

Holotype ♂ (figure 51*a*). *Length*: 2.6 mm; *breadth*: 1.1 mm. *Aedeagophore* (figure 40, plate 2). Siberia, Irkutsk oblast. Tibelti (Тибельти), Irkut valley 28 km west of Lake Baikal, 8–15. vi. 1970, R. B. Angus. In the Zoological Institute, Leningrad.

Paratypes: 245 Siberian specimens, all collected by R. B. Angus, and 9 Mongolian specimens, as follows:

93 (55 ♂♂, 38 ♀♀), same data as holotype; 58 (38 ♂♂, 20 ♀♀), Irkutsk oblast, Dachnaya, near Bolshoi Lug, 3–5. vi. 1970; 9 (6 ♂♂, 3 ♀♀), Irkutsk oblast, by the River Malaya Bystraya, Irkut valley 18 km west of Lake Baikal, 10. vi. 1970; 2 (1 ♂, 1 ♀), Irkutsk oblast, Bolshie Koty, by L. Baikal 20 km east of Listvyanka, 18–21. vi. 1970; 25 (15 ♂♂, 10 ♀♀), Siberia, Buryat A.S.S.R. Tunka, Irkut valley 90 km west of Lake Baikal, 12. vi. 1970; 43 (21 ♂♂, 22 ♀♀), Siberia, Yakutia. By the river Lena to 140 km upstream from Yakutsk, 27–29. vi. 1970; 2 (♂♂), Yakutia, Chuchur Muran (just outside Yakutsk), 30. vi–1. vii. 1970; 3 (2 ♂♂, 1 ♀), Yakutia, by the Vilyuyskiy Trakt (the road from Yakutsk to the River Vilyuy) to 55 km west of Yakutsk, 2–5. vii. 1970; 10 (6 ♂♂, 4 ♀♀), Yakutia, Olëkminsk, 7–13. vii. 1970; 9 (♂♂), Mongolia, Central Aimak. Kerulen, 45 km east of Somon Bajandelger, 1340 m above sea level. Exped. Dr Z. Kaszab, 1965. Coll. no. 307, 27. vii. 1965. In the Hungarian Museum of Natural History, Budapest.

The Siberian paratypes are at present all in my collection, but in due course specimens will be distributed to various museums, including the British Museum (Natural History) in London, the Hope Department of Entomology, Oxford, the Zoological Institute, Leningrad, and the entomological collections in Moscow, Irkutsk, Yakutsk and Novosibirsk.

This is a very common species in eastern Siberia, and I have seen so much material that it has been necessary to exclude most of it, including nearly all the Mongolian material brought back by Dr Kaszab's expeditions, from the type series. All references to *H. brevipalpis* in Siberia and Mongolia (e.g. Angus 1970*c*), unless complete misidentifications, refer to *H. aspericollis*.

As mentioned at the start of this description, *H. aspericollis* is very similar to *H. brevipalpis*, but is easily distinguished by the larger aedeagohpore, length 0.52–0.57 mm (figures 40–42, plate 36), as against 0.41–0.47 mm in *brevipalpis* (figure 49). These figures also show the difference in the relative lengths of the struts. *H. montenegrinus* Kuwert, from southeast Europe, has a larger aedeagophore, length 0.45–0.52 mm, but the paramere shape is different from both *brevipalpis* and *aspericollis*. The aedeagophores of the three species are shown by Angus (1970*a*, p. 134, figure 2, 5–7), but at that time I had not realized that they were three separate species.

Apart from the genitalic differences, *H. brevipalpis* and *montenegrinus* differ from *aspericollis* in the reduced granulation of the central area of the pronotum (often effaced, especially in *montenegrinus*), and in *H. brevipalpis* the elytral interstices are generally more than 1.5 times the width of the strial punctures, and the basal quarter of interstice 2 is not normally ridged as in *aspericollis*. These differences are shown in figure 51.

5. The age of the fossils

The material collected by the Krakow expedition to Starunia has been radiocarbon dated at the Smithsonian Institution, Washington, and this gives an age of 23255 ± 775 years B.P. (SI–642) (J. Pawłowski, personal communication, 4. v. 72). This means that they date from the full glacial of the last (Würm or Weichselian) glaciation.

The age of the Borislav fossils is less clear. According to I. K. Zahaikevitch (Lvov) (personal communication, 12. iv. 71), studying Łomnicki's work (in Polish), the deposits were thought to be aged about 300–350000 years, which would place them possibly in the early part of the penultimate (Riss or Saalian) glaciation. However, the Starunia remains were earlier thought to date from the greatest Polish glaciation, the 'Cracovien', which has been equated with the Alpine Riss or even Mindel (Szafer 1930, p. 20), and Zahaikevitch (personal communication, 21. vii. 71) says that there are at present new ideas on the subject, and that the age of the Borislav deposits may be less than was suggested by Łomnicki.

The Borislav specimens are somewhat mineralized, in contrast to those from Starunia, and although prolonged soaking in benzene removes some heavy oil from them, they remain unnaturally dark. They are also more impregnated with insoluble mineral matter, as is shown by the poorer clearing of balsam mounts made from Borislav material than Starunia ones (figure 14, plate 35, figures 21–23, plate 36). This could well be the result of different sedimentary environments in the two places, but it would also be consistent with the Borislav fossils having been embedded much longer in the pitchy silt, and in particular having endured the warmer conditions of the interglacial separating the Saalian and Weichselian glaciations.

A possible Saalian age of the Borislav deposits is also suggested by the fact that one of the *Helophorus*, *H. oblongus* LeConte, is otherwise known as a fossil from only two Pleistocene deposits, both from the early part of the Saalian (H. Kenward (Birmingham), personal communication, 8. vi. 71). It may also be noted that although there are many known insect assemblages from deposits of the Weichselian glaciation (see Coope, Morgan & Osborne 1971), there are very few from the Saalian, the only other one yielding a sizeable fauna being the Brandon Channel deposit described by Osborne & Shotton (1968). Although this deposit did not yield *H. oblongus*, it did have *H. praenanus*, another species present in the Borislav sample, and known from both Saalian and Weichselian deposits. It therefore seems that *H. oblongus* lived in Europe during the Saalian glaciation, but may not have been present in the later Weichselian. There is thus some reason for thinking that the Borislav fossils may be of Saalian age, but until further data are available the matter must remain open to question. There does, however, seem to be the intriguing possibility that fossil *H. oblongus* in Europe may be an indicator of Saalian deposits.

6. The Borislav fauna

One of the most curious features of the Borislav fauna is the small number of species present – only four *Helophorus*, and rather low numbers of other groups. The very good preservation of most of the material and the long series of some species, such as *H. sibiricus*, suggest that the site was both good for fossilization and fairly well sampled, and that whatever factor operated to restrict the number of species represented in the material was one which sorted them out at the time of deposition. At the moment there is no indication of what this may have been.

Although only four *Helophorus* species are recorded from the Borislav deposits, these indicate that they were laid down during cold conditions. If the present-day distributions of the four species are examined (figures 52, 53, 58, 60), it will be seen that only one species, *H. aquaticus*, lives in that area now, while the other three have distributions centred on areas of far colder climate. Further, it may be noticed that the range of *H. aquaticus* includes areas of far colder conditions than exist in the Lvov area today.

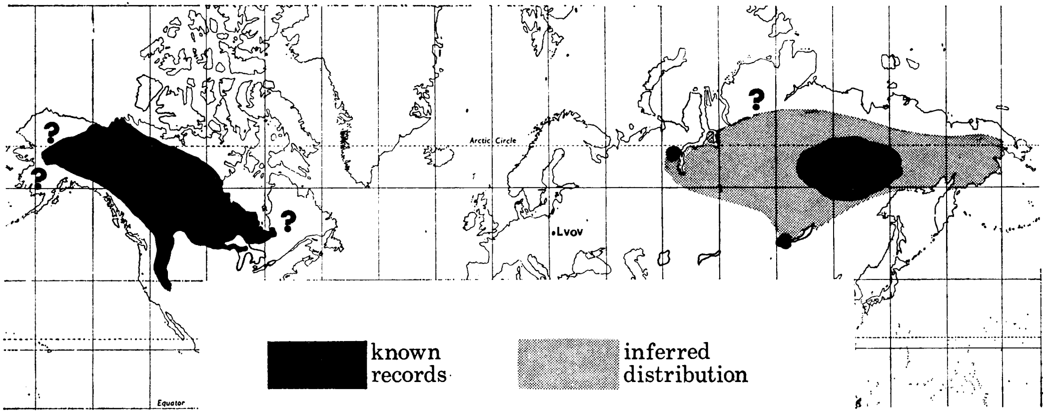


FIGURE 52. Modern distribution of *H. oblongus* LeConte.

As the fauna is so small, and its age uncertain, it is necessary to discuss here only the distribution of *H. oblongus*, as the other three species also occur in the Starunia deposits and will be considered in the discussion of that fauna. The present distribution of *H. oblongus* is shown on figure 52. It has an extensive range in North America, mainly northern, but extends southwards along the Rocky Mountains as far as California (McCorkle 1967). There are no records for western Alaska or Labrador, but as both these areas are only poorly known it is possible that it may occur there. In Siberia there are many records from the Yakutsk region, as well as one by Zaitzev (1953) from the tundra near Salekhard (specimen in the Zoological Institute, Leningrad). I took the species in heavily shaded pools in the taiga near Lake Baikal, so that this species is apparently widely distributed in the tundra and taiga regions of Siberia, the scattering of records reflecting a shortage of collectors rather than of beetles. It is interesting to note that in the southern part of its range it is apparently confined to the forest, while in Yakutia it was abundant in pools in open grassland.

If the Borislav fauna is really Saalian it is curious that *H. oblongus* should have occurred in Europe during this glaciation but not in the subsequent (Weichselian) one, as many Siberian species are known from Weichselian deposits.

7. THE STARUNIA FAUNA

There are four aspects of the Starunia fauna which are of particular interest. These are:

(1) As stressed in the introduction to this paper, the preservation of the fossils is so good that it has been possible not only to identify many of the specimens with complete certainty, but also to study intraspecific variation.

(2) The known age of about 23000 years for this fauna indicates that it dates from slightly before the coldest part of the last glaciation (see Coope *et al.* 1971, p. 96), so that in analysing

the fauna one is investigating the environmental régime of a period when the climatic conditions, at least in terms of the extent of the ice sheets, were known.

(3) This is, as fossil *Helophorus* faunas go, diverse, with nine species, all of whose environmental requirements are, to some extent, known. This permits a number of inferences about facets of the Starunia environment.

(4) There are in Britain numerous known and dated Weichselian fossiliferous deposits (Coope *et al.* 1971), and these may be compared with Starunia to give some indication of the effects of distance and time on the *Helophorus* of the two regions.

The present-day distributions of the Starunia *Helophorus* are shown on figures 53–61. It should be noted that most of Siberia is relatively little known, and collecting tends to be concentrated in the area round Lake Baikal, the Yakutsk region, and the far east (Maritime Territory). Nevertheless, there are some records from western Siberia, and a few from the northern part of the Urals. It is thus possible to indicate the approximate distributions of Siberian *Helophorus* species, but in many cases the ranges may be expected to be larger than indicated on the maps, especially towards the north and northwest. I have marked those areas where the species seem most likely to be discovered with question marks (?). All the Palaearctic distributions are based on specimens I have seen; New World distributions are taken from McCorkle (1967).

Four of the Starunia *Helophorus* live in the Starunia area at the present time, and these are considered first.

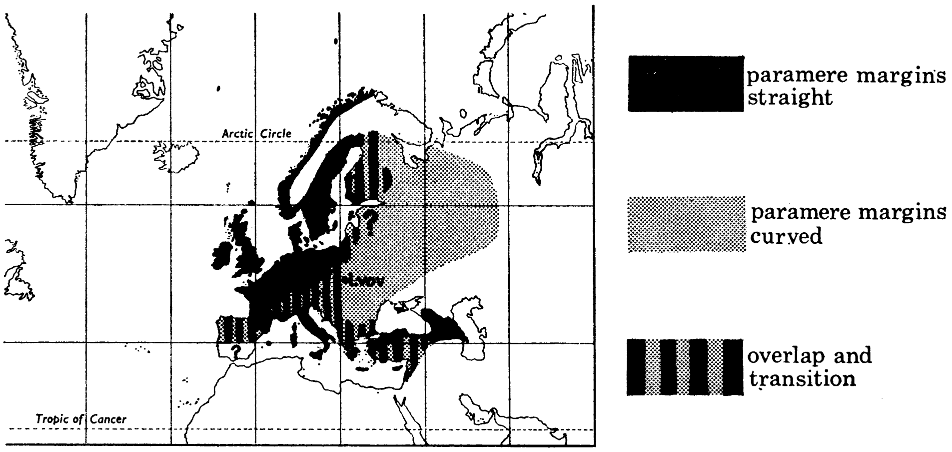


FIGURE 53. Modern distribution of *H. aquaticus* (L.) and its two races.

(*a*) *H. aquaticus* (L.)

This is by far the most numerous species in the sample, with material representing at least 130 individuals (see p. 309), and much of the material is very well preserved. The aedeagophores of Starunia specimens are shown in figures 21–23, plate 36 while figures 17–20 show the aedeagophores of modern specimens, and figures 24–26 show specimens from a British Pleistocene site at Dorchester on Thames (Oxfordshire), radiocarbon dated at 39000^{+1350}_{-1150} (Birm-333). The seventh abdominal sternites of fossil specimens from Starunia and Dorchester are shown in figures 9, 10, plate 35 and these show the same characteristic fine denticulation as modern specimens (figure 7).

H. aquaticus is a common species, widely distributed in Europe (figure 53), and its range extends northeast as far as Archangel, Ukhta (Komi A.S.S.R.) and Perm, but apparently not as far as the Pechora. This species is of particular interest as it exists as two distinct races, both of which can be recognized among the fossils. In western Europe the males have the outer margins of the parameres straight (figures 17, 18, plate 2), while in the east, and on high ground farther west, they are distinctly curved (figures 19, 20). The two forms intergrade where they meet.

The distributions of the two forms, and the areas of intergradation and overlap are shown on figure 53. All the British specimens I have seen, as well as those from lowland France, the Netherlands, southern Scandinavia and the Norwegian coast up to the Lofoten Islands have straight paramere margins, while those from Leningrad, Perm and other northern and middle Russian localities have these margins distinctly curved. There are thus two large areas with uniform populations, but between these is a fairly broad band in which both forms occur, and in which many specimens have the paramere margins only weakly curved. This transition zone extends over Finland and Karelia, where the most easterly specimens I have seen with weakly curved paramere margins are from the River Svir, between Lakes Ladoga and Onega. The transition zone extends south to southeast Poland (where a sample from Przemysl, about 120 km northwest of the Starunia site, included both forms (figures 18, 19, plate 36)), and over the Alps, the Carpathians and the Hungarian plain. I have not seen any specimens from the southern shore of the Gulf of Finland, but a single specimen from the island of Lavansaari, between Narva and Vyborg, has the parameres completely straight. Populations from Spain (where the species is apparently confined to high ground), the Balkans and most of Asia Minor have a mixture of both forms, with intermediates, but those from the Crimea and the Caucasus apparently consist entirely of the straight form, as do Italian and Greek populations, and those from the Mediterranean islands.

Thus the two races inhabit different areas and are connected by a clinal zone. The Starunia fossils include both races (figures 21 and 23, plate 36), as well as intermediates (figure 22), showing that 23000 years ago the transitional zone existed in the eastern Carpathians, as it does today (see above). However, British fossil material shows that the races are in fact much older than this. Specimens from Dorchester (dated at about 39000 years B.P.) all have curved paramere margins (figures 24–26), and I have seen a single specimen from an Eemian interglacial deposit in Lincolnshire (aged about 100000 years) in which the parameres are quite straight (M. Girling (Birmingham), unpublished data).

Whatever balance of selective factors gives rise to a situation in which two races within a species intergrade clinally, it is clear that this situation may not only be maintained for at least tens of thousands of years, but is also sufficiently stable for the geographical distributions of the races to alter radically without destroying the clinal structure.

(*b*) *H. grandis* Illiger

This species is represented by only one head and prothorax in the Starunia sample. However, the coarse and even granulation of the pronotum (figure 4, plate 35), and the expanded stem of the Y groove of the head, leave no doubt of its identity. This species is well known in British Pleistocene deposits, and the aedeagophore and seventh abdominal sternite of a fossil from the Dorchester site already mentioned are shown in figures 12 and 6, while figures 11 and 5 show those of the lectotype (Angus 1970*b*, p. 35), for comparison.

The present-day distribution of *H. grandis* is shown on figure 54. Like *H. aquaticus*, this species is widely distributed in Europe, though it does not extend quite so far to the northeast – I have seen no specimens from Ukhta, though it does occur at Syktyvkar and Archangel, and it is not present among d'Orchymont's material from Perm. The distributions of *H. grandis* and *aquaticus* differ principally in that *grandis* does not occur on the Hungarian steppe, or on high mountains. As a result of this the Mediterranean populations are to some extent isolated from those farther north, and, possibly because of this isolation, are differentiated into two subspecies, *H. g. maritimus* Rey and *H. g. syriacus* Kuwert. This complex has been discussed in an earlier publication (Angus 1970*b*), where the introduction of *H. g. grandis* into North America is also mentioned.

In the southwest *H. g. grandis* extends into northern Spain, where it is represented by a female from Reinosa, in d'Orchymont's collection. This specimen has the pronotal grooves slightly widened and deepened, suggesting a possible transition to *maritimus*. However, a lot more material is needed before this can be established. The most northerly Spanish *maritimus* I have seen is a male from Aranjuez, in the Helsinki museum.

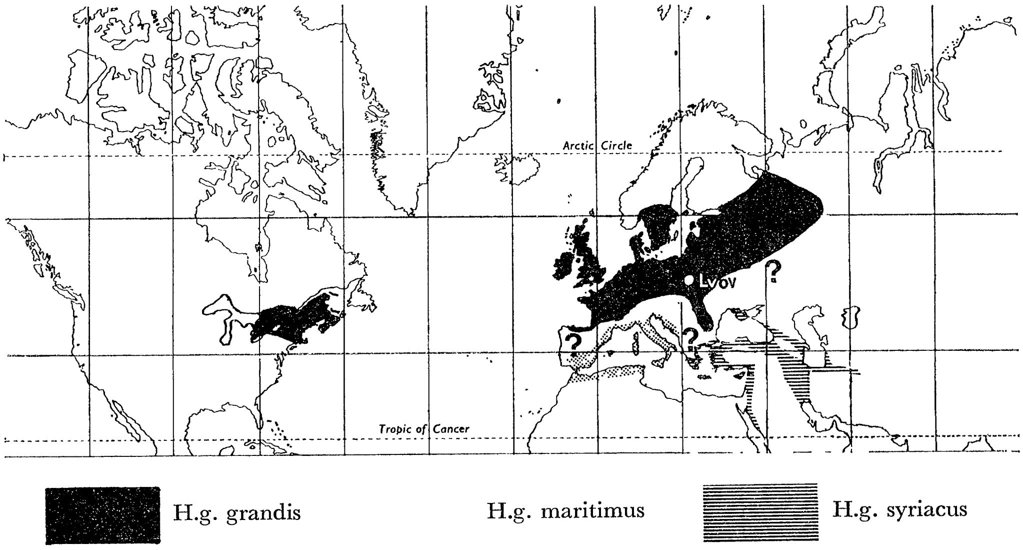


FIGURE 54. Modern distribution of the three subspecies of *H. grandis* Ill.

Farther east *H. g. grandis* extends southwards along the Carpathians, as confirmed by a specimen from Comana Vlasca, near Bucharest, in the d'Orchymont collection. It is thus possible that it interacts wth *H. g. syriacus* in this area. It will be seen from figure 54 that I have no material from northern Greece, Albania or Bulgaria, where *H. g. syriacus* and *maritimus* must meet.

It should be noted that all fossil *H. grandis* so far known are from deposits of the last glaciation and later. It would be particularly interesting to find this species in warmer interglacial deposits, as it is possible that in these times the subspecies *maritimus* and *syriacus* lived north of their present ranges, in which case their subspecific differentiation would have nothing to do with the present isolation of Mediterranean and northern populations. The known movement of the *H. aquaticus* cline (see above, p. 315) and the ready recognition of the subspecies of *H. grandis* on the form of the pronotum make this a promising field for investigation.

Both *H. aquaticus* and *H. grandis* live in shallow grassy pools. They have large mandibles and can strip the epidermis and parenchyma from grass which has been flooded. They must have some bare mud in which to place their egg cocoons.

(*c*) *H. glacialis* Villa

Both the specimens in the Starunia sample are very soft and pale, making their identification a little uncertain. The aedeagophores are shown in figures 36 and 37, plate 36. A modern Norwegian specimen is shown in figure 34, and a fossil from a British Late Glacial site at Orleton, Herefordshire, collected by Dr Coope, is shown in figure 35. The four aedeagophores may be seen to be broadly similar in size and in the proportions of their parts, despite the slight distortion of the Starunia specimens.

The present-day distribution of *H. glacialis* is shown on figure 55. The species is widely distributed in Europe, on low ground in the far north, and on mountains farther south, as far as the Sierra Nevada in Spain and Mount Olympus in Greece. In the Caucasus and mountains of Asia Minor *H. glacialis* is replaced by *H. guttulus* Motsch., *H. faustianus* Sharp and *H. abeillei* Guilleb., and in the mountains of Middle Asia by *H. longipennis* Gangl. Of this group of species, *glacialis* is the one most closely resembling the Starunia fossils.

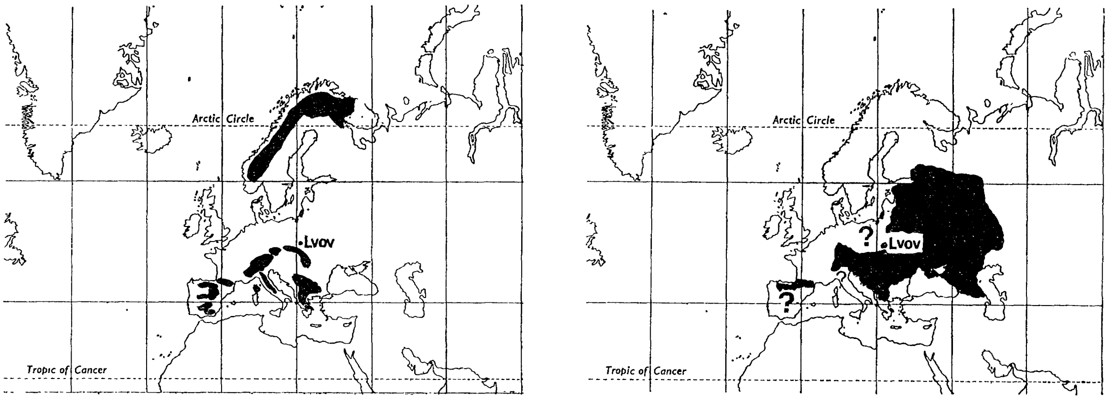


FIGURE 55, 56. Modern distributions of *H. glacialis* Villa (55) and *H. discrepans* Rey (56).

In northern Europe *H. glacialis* is a stenotherm, normally confined to the edges of snow patches, where the ground water is always near freezing-point and the bare earth matches the near black colour of the beetles, but I do not know whether there is always permanent snow in the more southern parts of its range.

(*d*) *H. discrepans* Rey

The Starunia sample contains only one specimen of this species. The aedeagophore (figure 33, plate 36) was slightly damaged in the course of dissection, but shape and size of all the components are the same as in the modern specimen shown in figure 32.

This is a species whose habitat changes within its distributional range (figure 56). In the east it is a pond species, and it was numerous in snow-melt pools round Leningrad in the spring of 1970. Farther west it is an inhabitant of mountain streams as well as upland pools. (Angus 1969, p. 6). It has not yet been found in British Pleistocene deposits, but it would be virtually impossible to recognize except by the aedeagophore.

The five remaining species, all mainly Siberian in distribution, differ among themselves in their detailed ranges. Two, *H. aspericollis* and *H. praenanus*, have very similar distributions (figures 57, 58), ranging over the cold continental part of Siberia and northern Mongolia.

They are not found in western Siberia, but as this area is not well known the exact limits of their ranges are not clear. The Reitter collection contains a single *aspericollis* (♀) from Tomsk, but the most westerly *praenanus* I know are from Kosh Agatch in the Altai. In the north, I have seen both species from Zhigansk, and *H. praenanus* has also been taken on the southeast Taimyr. Both species probably range some distance into Chukhotka in the east, but there are no records.

(*e*) *H. aspericollis* Angus

This species is well represented among the Starunia material, with fragments representing 14 specimens. There are nine aedeagophores, of which three are shown in figures 43–45, plate 36. The Starunia aedeagophores appear rather small for *H. aspericollis*, ranging in length from 0.48 to 0.53 mm, as against 0.52–0.57 mm in modern Siberian specimens. Siberian *aspericollis* range in length from 2.5 to 3.2 mm, while the lengths of the four measurable Starunia fossils are between 2.5 and 2.9 mm, and the other fragments also suggest small beetles. This small size does not appear to be a particular feature of Pleistocene populations as specimens from the Dorchester on Thames deposit already mentioned have aedeagophores whose lengths vary from 0.52 to 0.56 mm (figures 46–48), and the elytra and other fragments also suggest beetles of a size range similar to that of modern Siberian specimens.

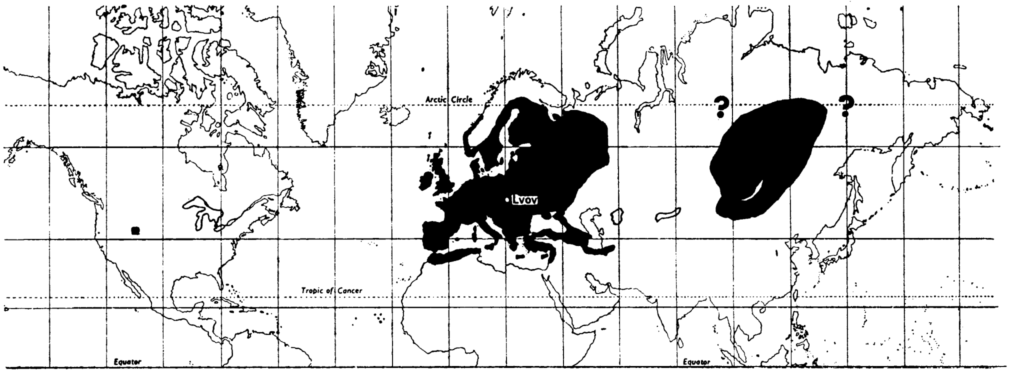


Figure 57. Modern distributions of *H. aspericollis* sp.nov. (East Siberia and Mongolia), and *H. brevipalpis* Bed. (Europe, N. Africa, W. Asia and introduced in Utah).

The discovery of the aedeagophores of Pleistocene *H. aspericollis*, first at Starunia then at Dorchester, is of particular interest as it confirms my suspicion that the '*brevipalpis*' from the Weichselian deposit at Brandon, Warwickshire, were of the 'Siberian style' (Coope 1970, p. 103). It was only as a result of detailed examination of the Siberian and European distributions of '*H. brevipalpis*' (both shown on figure 57), necessitated by the discovery of the Siberian form at Starunia, and recognition of the complete hiatus in the aedeagophore sizes of the two forms, that the separate specific identity of *H. brevipalpis* and *aspericollis* became apparent. Further, as pointed out by Dr Coope (personal communication), in the absence of a fossil record it might have been concluded from examination of the disjunct eastern and western distributions of the two forms, that these were populations forced apart in a retreat from the Pleistocene glaciations, and speciated as a result. Only the discovery of fossils of the Siberian *aspericollis* in western Europe in deposits of the Weichselian glaciation (and most probably the Saalian as well as I have seen pronota almost certainly belonging to *aspericollis* from the Brandon

Channel deposit, attributed to that glaciation by Osborne & Shotton (1968)) shows that this cannot be the cause of the speciation.

In eastern Siberia *H. aspericollis* occurs in shallow grassy pools, where it may be exceedingly abundant.

(*f*) *H. praenanus* Łomnicki

This is another species represented by only one specimen in the Starunia sample. The aedeagophore is shown in figure 28, plate 36, and may be compared with the fossil lectotype, from Borislav (figure 27), and a modern Siberian specimen (the lectotype of *H. jacutus* Popp.), shown in figure 29. *H. praenanus* is well known as a fossil in British Weichselian deposits, where it is often very numerous (Coope 1968), and is also present in the Saalian Brandon Channel deposit (Osborne & Shotton 1968, p. 421 and figure 6, plate 20). The pronotum of this species, with its reduced granulation, narrow grooves, evenly curved sides and yellow anterior margins (all shown very clearly in Osborne & Shotton's figure) is very distinctive. This species is present, though not abundant, in the Dorchester deposit already mentioned.

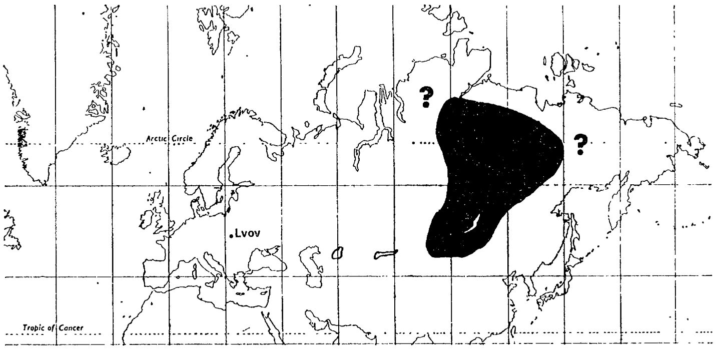


Figure 58. Modern distribution of *H. praenanus* Łom.

H. praenanus, like *aspericollis*, appears to be characteristic of grassy pools in eastern Siberia. Its distribution (figure 58) is entirely cold continental.

(*g*) *H. browni* McCorkle

The aedeagophore of the single Starunia fossil is shown in figure 31, plate 36, and that of the holotype, described in Angus (1970*c*), from northern Canada, is shown in figure 30. The Starunia specimen fossilized with the aedeagophore extruded, and the left paramere is missing. However, the rest of the aedeagophore is so distinctive that there can be no doubt of its identity.

The discovery of *H. browni* as a fossil at Starunia is of particular interest as this is a species not yet found in British Pleistocene deposits. The pronotum, reddish in colour and fairly granulate, is sufficiently distinctive for the species to be at least suspected, even if not positively identified, as a fossil. The present distribution of *H. browni* (figure 59), partly overlaps those of *H. aspericollis* and *praenanus*, but it has not been found in the Altai, and it is evidently rare in northern Mongolia where it was not taken by Dr Kaszab's expeditions, though it occurs in the mountains near Ulan Bator. However, the main difference is that *browni* is found on Kamchatka and in the Maritime Territory of Siberia, as well as along the arctic coast of northwest Canada and Alaska – all cold coastal areas. The northern and western limits of its Siberian distribution are not clear. The importance of its occurrence in maritime areas will be discussed in the comparison of the Starunia fauna with British Pleistocene assemblages.

The habitat of *H. browni*, like that of so many *Helophorus* species, seems to be shallow grassy pools.

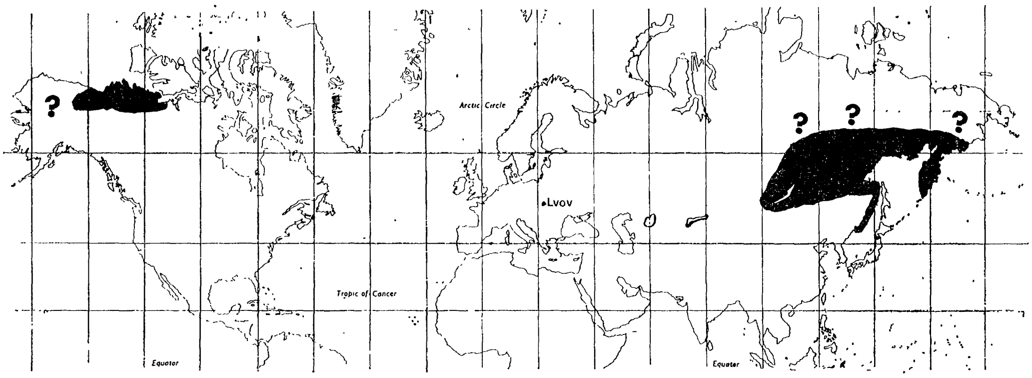


Figure 59. Modern distribution of *H. browni* McCorkle.

(*h*) *H. sibiricus* Motsch

This species is represented by only a single elytron in the Starunia sample. The elytron may be identified by the broad flank, strong ridging of the alternate interstices and long intercalary stria, as well as the size and shape. *H. sibiricus* is present in both Full Glacial and Late Glacial sites in Britain (Coope 1968, 1970).

As is shown on figure 60, the modern distribution is very wide, extending over most of Siberia, as well as Scandinavia and the northern part of European Russia, and Alaska and northwest Canada. This is another species whose habitat varies in different parts of its range. In Scandinavia it appears to be characteristic of the edges of rivers, but in Siberia it is also found in grassy pools, particularly those resulting from melting snow (Angus 1970*b*, p. 24).

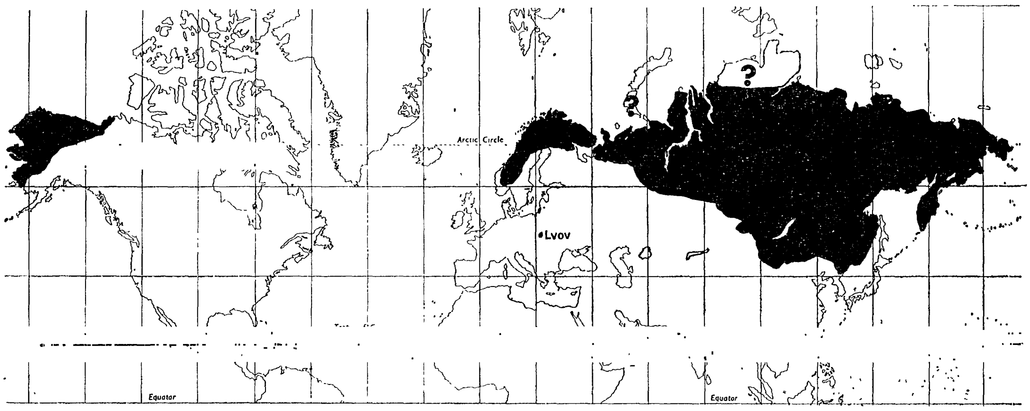


Figure 60. Modern distribution of *H. sibiricus* Motsch.

(*i*) *H. orientalis* Motsch

This is a particularly interesting species as over most of its range it is parthenogenetic (Angus 1970*a*). There are two specimens present in the Starunia sample, both recognizable on the pronotal sculpture, with the reduced granulation of the internal intervals. One of these pronota is shown in figure 3, plate 35. The recognition of fossil *H. orientalis* is not easy as reduction of the pronotal granulation is not uncommon in *Helophorus*, and detailed comparison of the pronotal size, shape and colour pattern is necessary. This is discussed by Angus (1970*a*). Both *H. flavipes* F. and *H. carsoni* Angus may have the pronotal sculpture similar to that of *orientalis* but the former lacks the pale margins of *orientalis* and in the latter the internal intervals lack the rounded raising of the central portion, which tends to be characteristic of *orientalis*. Further, in *H. carsoni* the pronotal width is generally over 1 mm, but in *orientalis* it is usually less.

One of the Starunia fossils has one antenna eight-segmented and the other nine-segmented – the only specimen in which I have seen this condition. However, eight-segmented antennae do sometimes occur, on one or both sides, in species in which they are normally nine-segmented. Occasionally a population may show an exceptional frequency of this condition, as, for instance, the Odessa population of *H. longitarsis* Woll. (Angus 1971).

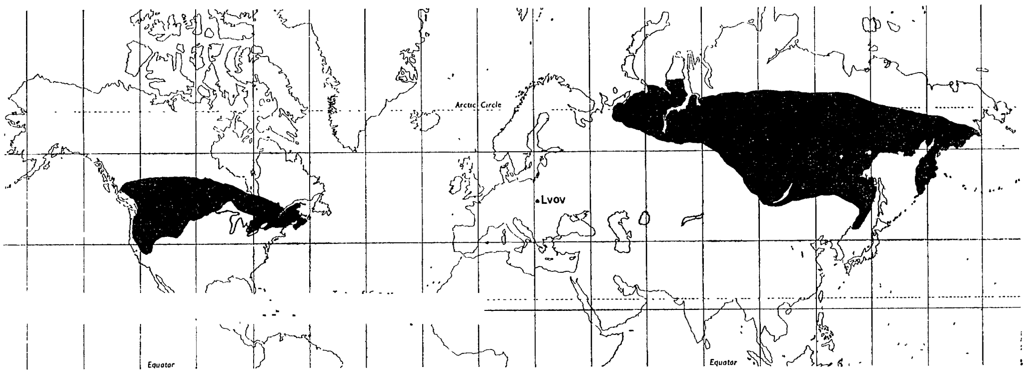


Figure 61. Modern distribution of *H. orientalis* Motsch.

The present-day distribution is shown on figure 61. It is very curious that while in the Old World this is a distinctly northern species (especially at the western end of its range), in North America it has an appreciably more southern distribution.

This is another grassy pool species, and is an important colonist of temporary pools, where it may have two or more generations in a summer (Angus 1970*a*).

8. The Starunia fauna as a whole

As will be apparent from the preceding account of the *Helophorus* species found as fossils in the Starunia deposit, most are characteristic of small grassy pools, and these must have been an important part of the environment there. In much of Siberia there are very extensive pools of this sort left by the spring snow melt, and these last for 6 weeks or so before drying up for the summer. All the Siberian *Helophorus* species included in the fauna are abundant in such pools in Siberia today, and *H. aquaticus*, *grandis* and *discrepans* are numerous in similar pools in European Russia.

The presence of *H. glacialis* indicates persistent snow fields or patches which went on melting all summer to provide cold water on a dark background. As the area lies in the foothills of the Carpathians this is not surprising. Today *H. glacialis* is still present in the Carpathians, but at higher altitudes.

Since Starunia is situated in the Carpathian foothills it is possible that *H. sibiricus* and *discrepans* were associated with the cold rivers.

Turning to the broader climatic implications, the picture is far more complex. Thus four of the Starunia *Helophorus* are at present widely distributed over Europe, two are confined exclusively to the cold continental area of east Siberia and northern Mongolia, one ranges over both the cold continental and cold coastal areas of Siberia, as well as the northwest coast of Canada, while the remaining two species have wide distributions, though mainly in areas of cold or very cold climate. All the species – even the two lowland European ones (*aquaticus* and *grandis*) – have some areas of very cold climate included in their ranges. But it is important to note that in no modern fauna is there a combination of very cold continental (east Siberian) and relatively temperate (European) elements, such as are represented in the Pleistocene Starunia fauna, and in faunas from British Pleistocene deposits. Thus these glacial environments are not entirely comparable with those of present-day central or eastern Europe, the Arctic, or cold continental Siberia, but combine elements of all of these. They also lack any definitively west-European elements.

One further point of interest is the number of *Helophorus* species known from the Starunia deposit – nine. In my experience, if the *Helophorus* from a fairly restricted area are sampled, the number of species taken is between nine and thirteen, and this holds for areas of Britain, the Leningrad Region, and both steppe and taiga regions of Siberia. It thus appears that the sample of *Helophorus* from Starunia probably contains most of the species present at that time.

9. Comparison of the Starunia *Helophorus* fauna with the Orthoptera

Zeuner (1934) gives an account of the fossil Orthoptera collected by the 1929 Krakow expedition to Starunia, and as these are the only other fossil insects from there to have been studied to date, it is interesting to compare the composition of the orthopteran fauna with the *Helophorus*.

The Starunia Orthoptera, like the *Helophorus*, are in general very well preserved, with several complete specimens included among the material. Zeuner gives positive identifications of six species, with tentative ones of two more, and description of one species as new. This is distinguished from a species at present living in the high mountains of Montenegro, and it is suggested that the new species may be found living somewhere in Asia.

Of the six positively identified species, three are widespread in the mountainous regions of central and southern Europe, and one of these, *Aeropus sibiricus* L., also lives in northern England. Only one of these species, *Polysarcus denticaudatus* Charp., does not extend east of Europe. The other two range over the Caucasus, the mountains of Middle Asia and Siberia, and inhabit lower ground in the northern and eastern parts of their ranges.

A fourth species, *Podisma frigida* Bohem., is an arctic-alpine in Europe, being known in Lapland and Scotland, and in the highest valleys of the Alps. In the east its range extends over the Russian plain to Siberia, Mongolia and Alaska.

The two remaining species have more eastern distributions. *Podismopsis altaica* Miram. lives in the Altai, and mountains eastwards to Korea. *Chorthippus angulatus* Tarb. is known only from the high mountains of Middle Asia (Kirgiz Mts).

Compared with the *Helophorus*, the Starunia Orthoptera are strikingly montane, or at least upland, in their modern distributions. There are no species with wide distributions over lowland Europe, such as are shown by *Helophorus aquaticus* and *grandis*. Conversely, there are no *Helophorus* from Starunia which are at present confined to high ground. This may be the reason for the complete absence of any Middle Asian element in the *Helophorus* fauna. What the Starunia *Helophorus* and Orthoptera do show in common is a generally cold-adapted assemblage of species with a number of predominantly eastern forms. Although both groups include species whose present ranges extend into the Arctic, no species is confined to that region. It seems likely that the predominance of montane species among the Orthoptera reflects the same continentality of climate that is shown by such *Helophorus* as *H. aspericollis* and *praenanus*.

10. Comparison of the Starunia *Helophorus* fauna with faunas obtained from British Pleistocene deposits

The radiocarbon date of 23 255 ± 775 years B.P. for the Starunia fossils means that they date from just before the onset of the coldest phase of the last glaciation. In their chart of Weichselian climate, Coope *et al.* (1971, p. 96) show the period between 25 and 22 000 years ago as a time of transition between the cold continental conditions which had prevailed since about 40 000 years ago and the period of the maximum extent of the Weichselian ice sheets.

There are no known British insect-bearing deposits dating from this transitional period. The deposit from the Lea Valley in Hertfordshire, dated at 21 530 ± 480 years B.P. (Birm-238), yielded very few insects (G. R. Coope, personal communication), and evidently reflects far more severe conditions than those pertaining when the Starunia deposits were laid down. It thus appears more useful to compare the Starunia fauna with that occurring in Britain during the cold continental period preceding the glacial maximum. Coope *et al.* (1971, p. 92) refer to this as the 'tundra period' of the Weichselian glaciation, and list many dated faunas aged between about 40 000 and 25 000 years. Immediately preceding this tundra period is the Upton Warren Interstadial, with warmer conditions and fewer cold elements in the fauna.

In comparing British deposits with Starunia, the discussion will be limited to deposits dating from this tundra period. The faunas from sites dating from this period are all broadly similar (Coope *et al.* 1971, p. 91), and in discussion of them special attention will be paid to the faunas from the Brandon Terrace (Coope 1968), the Tame Valley sites (Coope & Sands 1966), and the newly discovered site at Dorchester on Thames, Oxfordshire, about 14 km southeast of Oxford. This site, radiocarbon dated at $39\,300^{+1350}_{-1150}$ B.P. (Birm-333), dates from the very beginning of the tundra period, and has yielded unusually large numbers of fossil abdomens, from many of which it has been possible to extract aedeagophores. The beetle fauna is typical of cold tundra period deposits (G. R. Coope, personal communication).

H. aquaticus, *grandis* and *aspericollis* are present in varying numbers in all these deposits, but *praenanus* is not known from the Tame Valley. *H. sibiricus* is numerous in the Brandon and Tame Valley material, but scarce at Dorchester. In Britain this species tends to be abundant in the cold phases of the Late Glacial period. *H. orientalis* is fairly numerous at Brandon and abundant at Dorchester. *H. glacialis* is not known from tundra period deposits, but two of the Tame Valley sites yielded heads and pronota which may belong to this species. However, these show slight differences from undoubted *glacialis* fossils from the Late Glacial, and it is possible that they do not belong to this species. This cannot be resolved on the material at present available.

The Starunia sample contains two *Helophorus*, *H. discrepans* and *H. browni*, which have not as yet been found in British deposits, though *H. discrepans* would not be detected unless the aedeagophore was found.

The Dorchester deposits have yielded one species not present in the Starunia sample, and not yet discovered as a fossil elsewhere in Britain. This is *H. mongoliensis* Angus. The Dorchester material includes two abdomens with aedeagophores, and one of which had the pterothorax and elytra associated with it. There is also at least one prothorax. The aedeagophore of one of the fossils is shown in figure 39, plate 36, while figure 38 shows the holotype. This species was described by Angus (1970*c*). It is an inhabitant of mountain streams in the northern part of Mongolia, the Altai and the central Tian Shan. Thus its distribution lies slightly to the south of those of *aspericollis* and *praenanus* (which have quite different habitats), although there is quite a large overlap. *H. mongoliensis* represents a distributional type not found among the Starunia *Helophorus*, and it is possible that in the Dorchester sample it is a relict from the warmer Upton Warren Interstadial.

The apparent absence of *H. glacialis* in tundra period deposits in midland England suggests that there was not extensive winter snow which gradually melted through the summer. Coope *et al.* (1971) suggest that the average summer temperature during this period was only marginally higher than during the subsequent maximum extension of the ice sheets. They suggest that the absence of sufficient moisture was the factor preventing massive glaciation at this time. They further suggest that this could have been the result of a prevailing easterly airstream, and this may well be the factor enabling species now living in the cold continental area of Siberia to have lived so far west at that time.

The factor triggering the onset of the maximum extension of the ice sheets is thus suggested to have been a switch to a mainly westerly oceanic airstream. The presence of *H. glacialis* at Starunia may well reflect increasing snowfall as the prevailing airstream gradually became moister, leading up to the glacial maximum.

The difference in prevailing airstream between the tundra period whose British deposits are under discussion, and the transition to the wetter glacial maximum, in the course of which the Starunia deposit was laid down, may be the factor enabling *H. browni* to live at Starunia, but not in Britain – if the absence from British deposits is genuine.

Although *H. browni* today lives over much of the cold continental area of Siberia, it also has an extensive cold-coastal distribution – and at this point it should be stressed that a high arctic environment is of necessity cold-coastal. It may also be noted that *H. browni* is apparently most abundant in the area immediately round Lake Baikal, where the lake itself exerts a modifying influence on the continentality of the climate (Kozhov 1963, p. 115), and is much scarcer in Yakutia and rare in Mongolia (Angus 1970*c*, p. 281, gives an old record of three specimens from near Ulan Bator. This is confirmed by three further specimens, all from near Ulan Bator, taken by recent Soviet and East German expeditions). It is apparently numerous on Kamchatka and is well represented among material from the Maritime Territory of Siberia. It appears to be a conspicuous member of the beetle fauna of the arctic of Alaska and northwest Canada, and it is to be expected that this species will be discovered in the high arctic of eastern Siberia.

If, as already suggested, the Starunia deposit was laid down at a time when the prevailing airstream was becoming wetter, the climatic regime may have been in some respects like the eastern seaboard of Siberia. Starunia lies well away from the coast, and rather south of the British sites. Thus it would not be expected to have an extreme arctic environment – which might be associated with *H. splendidus* J. Sahlberg, a species today virtually confined to the arctic coastal plains of Siberia and western Canada. What *H. browni* may represent at Starunia is a faunal element associated with cold coastal environments, but less strictly so than *splendidus*.

It is therefore of particular interest to note that *H. splendidus* occurs as a fossil in a deposit aged about 14000 years (the very end of the maximum glaciation) at Glanllynnau in North Wales (Coope & Brophy 1972). It therefore seems likely that if *H. browni* is to be found in Britain it will be in deposits of this age.

Finally, once again it must be stressed that the climatic factors, as reflected in insect distributions, are complex and interacting. Study of various species known to have occurred in a given area at various times may reveal aspects of past climates, and as the number of species, areas and times increases, a coherent picture is gradually emerging.

This study was made possible as a result of my being able to work on material, both modern and fossil, in the Soviet Union. I thank the Royal Society and the Academy of Sciences of the U.S.S.R. for arranging for me work in Russia under their exchange scheme. I am particularly grateful to Dr O. L. Kryzhanovskiy (Leningrad) for all his assistance in my work in Russia, and to Dr I. K. Zahaikevitch (Lvov) for facilities to study the Łomnicki collection in Lvov. I also thank Professor K. Kowalski and Dr J. Pawłowski (Krakow) for the loan of the *Helophorus* brought back by the 1929 expedition to Starunia and information about the deposit there, and the curators of the various European museums which have lent me their *Helophorus*.

I am especially grateful to Dr G. R. Coope (Birmingham) for all his advice and helpful criticism of this manuscript, and for his unfailing generosity with both material and information resulting from his own work on Pleistocene Coleoptera. I thank Professor G. C. Varley for facilities to work in the Hope Department of Entomology, and Professor J. W. S. Pringle for the use of facilities in the Department of Zoology, Oxford. The photographs were taken by Mrs S. Phipps, of the Zoology Department, to whom I am very grateful. I also thank Mrs R. Wise, of the Hope Department, for drawing the beetles shown in figure 51.

Finally, I thank the Science Research Council for a Research Fellowship in the course of which this work has been carried out.

REFERENCES

Angus, R. B. 1969 Revisional notes on *Helophorus* F. (Col., Hydrophilidae). 1. General introduction and some species resembling *H. minutus* F. *Entomologist's mon. Mag.* **105**, 1–24.

Angus, R. B. 1970*a* *Helophorus orientalis* (Coleoptera: Hydrophilidae), a parthenogenetic water beetle from Siberia and North America, and a British Pleistocene fossil. *Can. Ent.* **102**, 129–143.

Angus, R. B. 1970*b* A revision of the beetles of the genus *Helophorus* F. (Col., Hydrophilidae), subgenera *Orphelophorus* d'Orchymont, *Gephelophorus* Sharp and *Meghelophorus* Kuwert. *Acta zool. fenn.* **129**, 1–62.

Angus, R. B. 1970*c* Revisional studies on east palaearctic and some nearctic species of *Helophorus* F. (Coleoptera: Hydrophilidae). *Acta zool. hung.* **16**, 249–290.

Angus, R. B. 1971 Revisional notes on *Helophorus* F. (Col., Hydrophilidae). 3. Species resembling *H. strigifrons* Thoms. and some further notes on species resembling *H. minutus* F. *Entomologist's mon. Mag.* **106** (1970), 238–256.

Balfour-Browne, W. A. F. 1958 *British water beetles* 3. London: Ray Society.

Coope, G. R. 1968 An insect fauna from Mid-Weichselian deposits at Brandon, Warwickshire. *Phil. Trans. R. Soc. Lond.* B **254**, 425–456.

Coope, G. R. 1970 Interpretations of Quaternary insect fossils. *A. Rev. Ent.* **15**, 97–120.

Coope, G. R. & Brophy, J. A. 1972 Late Glacial environmental changes indicated by a coleopteran succession from north Wales. *Boreas* **1**, 97–142.

Coope, G. R., Morgan, A. & Osborne, P. J. 1971 Fossil Coleoptera as indicators of climatic fluctuations during the last glaciation in Britain. *Palaeogeography, Palaeoclimatol. Palaeoecol.* **10**, 87–101.

Coope, G. R. & Sands, C. H. S. 1966 Insect faunas of the last glaciation from the Tame Valley, Warwickshire. *Proc. R. Soc. Lond.* B **165**, 389–412.

Kozhov, M. M. 1963 *Lake Baikal and its life*. The Hague: Junk.

Kuwert, A. 1866 General-Uebersicht der Helophoren aus Europa und angrenzenden Gebiete. *Weiner ent. Ztg* **5**, 221–228.

LeConte, J. L. 1850 General remarks upon the Coleoptera of Lake Superior, in Agassiz. *Lake Superior* **4**, 201–242. New York.

Linnaeus, C. 1758 *Systema Naturae. Editio decima reformata*. Stockholm.

Łomnicki, A. M. 1894 Pleistocenskie owady z Borysławia. (Fauna Pleistocenica insectorum Boryslaviensium). *Wydaw. Muz. Dzieduszyck.* **4**, 3–116.

Łomnicki, A. M. 1914*a* Topographical and geological relationships of the Starunia Fossils. *Wydaw. Muz. Dzieduszyck.* **15**, 12–24. (In Polish.)

Łomnicki, A. M. 1914*b* The invertebrata of the Mammoth shaft. *Wydaw. Muz. Dzieduszyck.* **15**, 37–89. (In Polish.)

McCorkle, D. V. 1967 A revision of the species of *Elophorus* Fabricius in America north of Mexico. University of Washington Ph.D. thesis, Seattle.

Motschulsky, V. 1860 *Reisen und Forschungen im Amur-Lande in den Jahren 1854–56 von Dr. Leopold v. Schrenck*. **2** (2). *Coleopteren*. St Petersburg: Imperial Academy of Sciences.

Nowak, J. & Panow, E. 1930 The geological conditions of the Starunia excavations. The second Woolly Rhinoceros from Starunia. *Bull. int. Acad. pol. Sci. Lett.* (B, Supplement), 1–7.

Osborne, P. J. & Shotton, F. W. S. 1968 The fauna of the channel deposit of early Saalian age at Brandon, Warwickshire. *Phil. Trans. R. Soc. Lond.* B **254**, 417–424.

Poppius, B. 1907 Beiträge zur Kenntnis der Coleopteren-fauna des Lena-Thales in Ost-Sibirien. 3. Gyrinidae, Hydrophilidae, Georyssidae, Parnidae, Heteroceridae, Lathridiidae und Scarabaeidae. *Öfvers. Vetenskaps. Soc. Förh.* **49** (1905–6) (2), 1–17.

Raciborski, M. 1914 The flora of the Mammoth shaft at Starunia. *Wydaw. Muz. Dzieduszyck.* **15**, 27–29. (In Polish.)

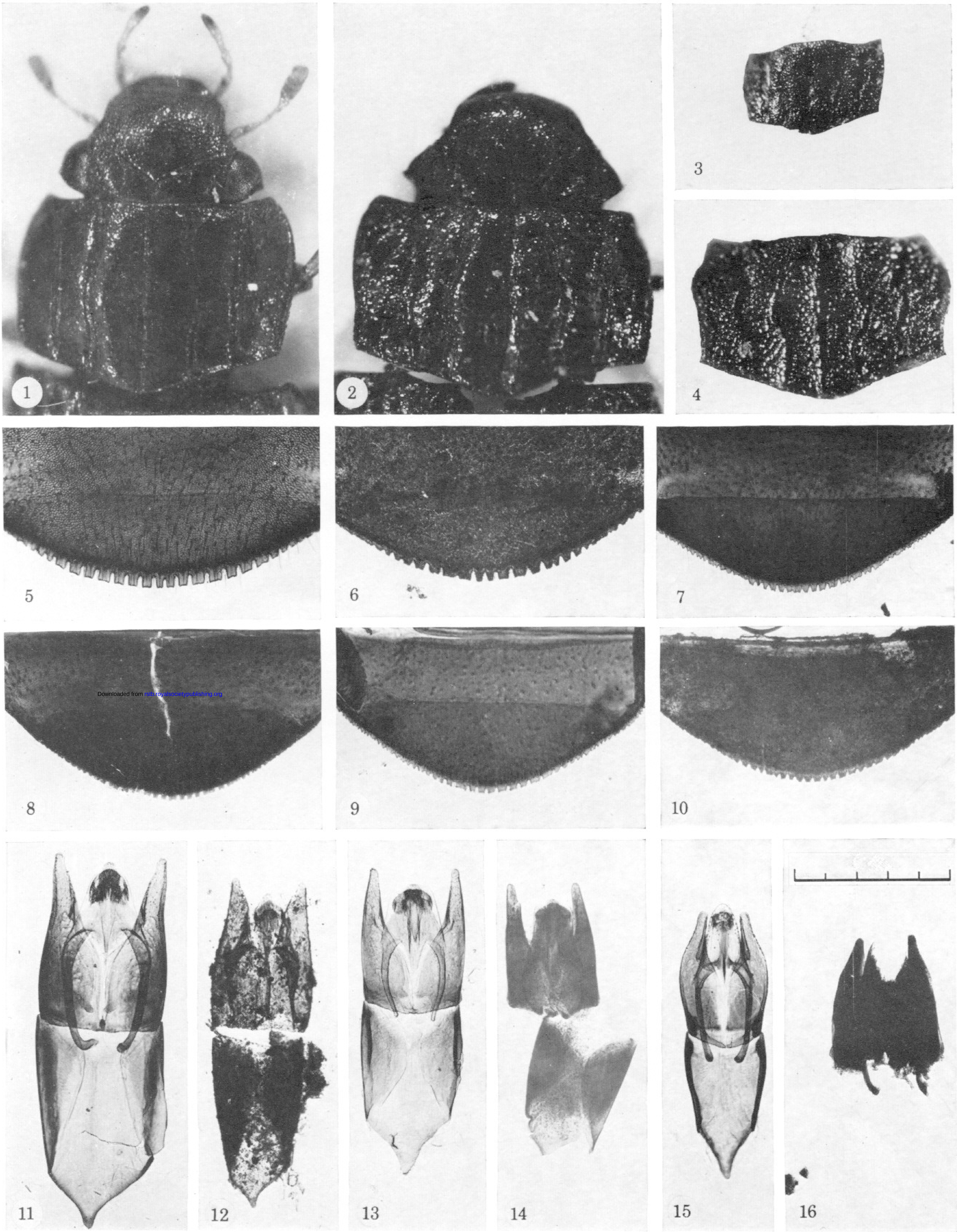
Stach, J. 1930 The second Woolly Rhinoceros from the diluvial strata of Starunia. *Bull. int. Akad. pol. Sci. Lett.* (B, Supplement), 21–47.

Szafer, W. 1930 The diluvial flora in Starunia. *Bull. int. Akad. pol. Sci. Lett.* (B, Supplement), 12–21.

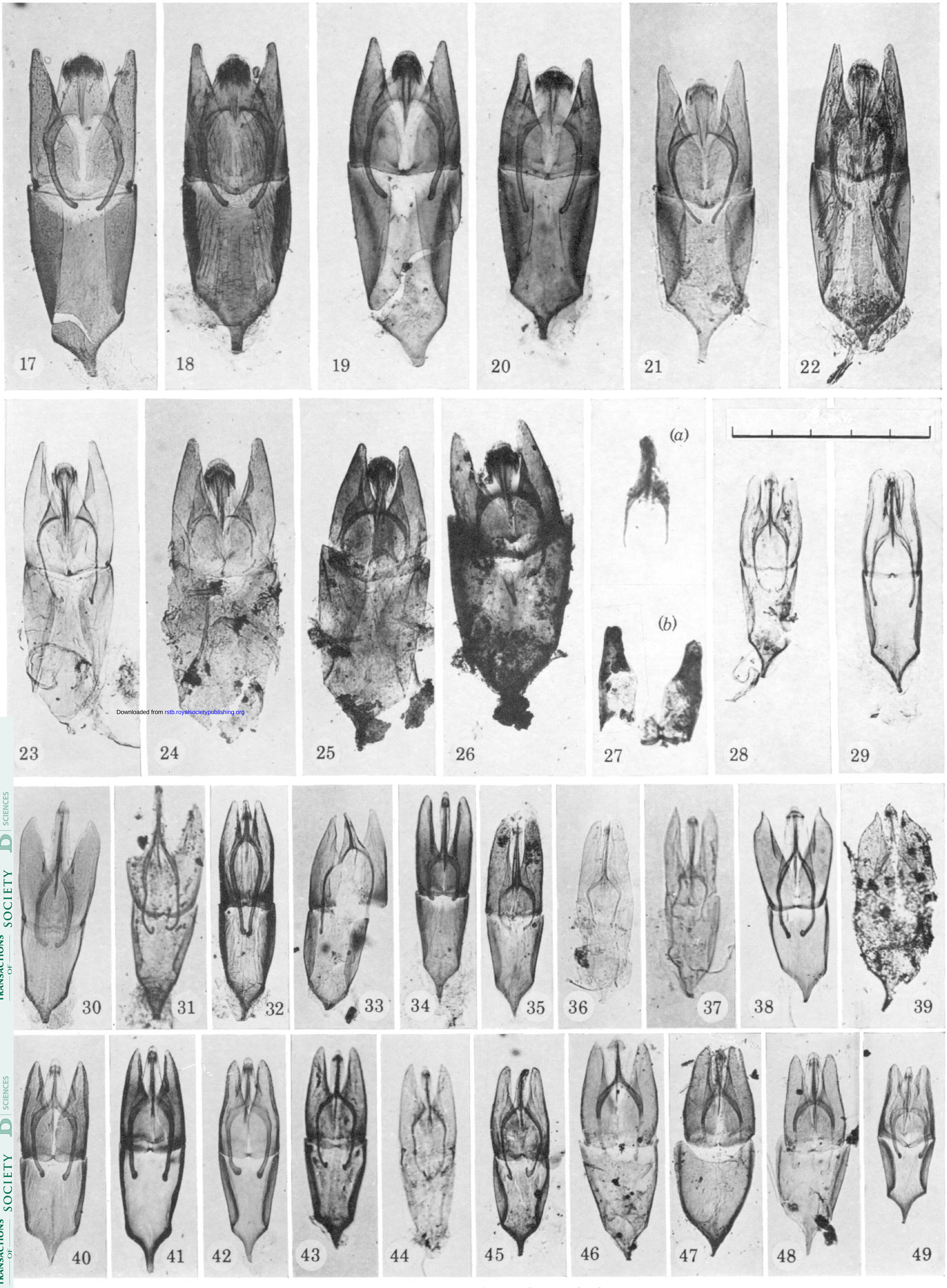
Zaitzev, F. A. 1910 Beiträge zur Kenntniss der Wasserkäfer des Ostens von Nordsibirien. Haliplidae, Dytiscidae, Gyrinidae, Hydrophilidae, Georyssidae, Dryopidae und Heteroceridae. *Zap. imp. Akad. Nauk.* (8): **18** (9), 11–52.

Zaitzev, F. A. 1953 On the water beetle fauna of the Polar Urals and Karskaya Tundra. *Ent. Obozr.* **3**, 226–232. (In Russian.)

Zeuner, F. 1934 Die Orthopteren aus der diluvialen Nashornschicht von Starunia (polnische Karpathen). *Starunia* **3**, 1–17.



FIGURES 1 TO 16. For legends see facing page



FIGURES 17 TO 49. For legends see facing page