Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic algae

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A large number of stream-dwelling animals feed on epilithic algae and must scrape or brush off food that is firmly attached to rough stones. The mouthparts of these highly specialized alga grazers are equipped with brushes, rakes, gouges, excavators, and rasps. Because they scrub across the rough substratum, these different types of feeding apparatus all become extremely worn down after a short time. The delicate bristles of brushes, the prongs of rakes, and the fine structures of rasps abrade swiftly, and often completely disappear after having been used for removing epilithic algae from stones. The blades of gouges and the scoops of excavators also wear down, but in this case abrasion usually causes only the shortening of these relatively solid tools and does not so strongly impair their effectiveness. Specific adaptations have been evolved to deal with the problem of wear. Either the grazing animals are able to repair their mouthparts frequently, or their feeding apparatus is constructed in such a way that its effectiveness is guaranteed for a long time despite the wear. Typical defects arising from use, and adaptations to wear, were studied comparatively by scanning electron microscopy of different alga grazers: insects of different orders (Ephemeroptera: *Rhithrogena*, *Epeorus*, *Ameletus*, *Baetis*, *Lepeorus*; Plecoptera: *Brachyptera*; Coleoptera: *Limnius*; Diptera: *Liponeura*, *Oxycera*), the isopod *Ligia italica*, the snail *Ancylus fluviatilis*, and the tropical fish *Garra taeniata*. Laboratory experiments with mayfly larvae showed that the mouthparts wear down when they are used to scrape a rough substratum. There was no evidence that moulting intervals were shortened by abrasion of feeding structures in mayfly larvae.

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Un grand nombre d'animaux d'eau courante se nourrissent d'algues épilithiques qu'elles doivent râcler ou frotter pour les détacher des pierres rugueuses. Les pièces buccales de ces brouteurs très spécialisés sont munies de brosses, raclettes, gouges, curettes et râpes. À force de se frotter contre le substrat rugueux, tous les types de pièces buccales s'usent très rapidement. Les soies délicates des brosses, les dents des raclettes, et les fines structures des râpes deviennent très usées et disparaissent parfois totalement après avoir servi à détacher les algues épilithiques. Les lames des gouges et les cuillères des curettes s'usent également, mais l'action abrasive n'entraîne ordinairement qu'un raccourcissement de ces outils plutôt solides et n'entrave pas autant leur efficacité. Des adaptations spécifiques sont venues pallier au problème de l'usure. Les animaux brouteurs peuvent régénérer leurs pièces buccales fréquemment ou alors leur appareil buccal est fait de telle façon que son efficacité est assurée pour longtemps en dépit de l'usure. Les défauts ordinairement reliés à l'usure et aux adaptations à l'usure chez différents types de brouteurs ont fait l'objet de comparaisons au microscope électronique à balayage : insectes de divers ordres (éphéméroptères : *Rhithrogena*, *Epeorus*, *Ameletus*, *Baetis*, *Lepeorus*; plécoptères : *Brachyptera*; coléoptères : *Limnius*; diptères : *Liponeura*, *Oxycera*), l'isopode *Ligia italica*, le gastropode *Ancylus fluviatilis* et le poisson tropical *Garra taeniata*. Des expériences de laboratoire sur des larves d'éphémères ont révélé que les pièces buccales s'usent lorsqu'elles sont utilisées pour râcler un substrat rugueux. Les intervalles entre les mues ne semblent pas avoir été raccourcis à la suite de l'usure des structures buccales chez les larves d'éphémères.

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Introduction

Thin epilithic layers of algae are one of the most important food resources in fast-running streams. At the stream bottom, nearly all surfaces of stones exposed to light are coated with a firmly adhering film mainly composed of diatoms and other single-celled algae. Animals feeding on this "pasture" need highly specialized mouthparts for scraping, collecting, and grinding their food (Arens 1989). To detach the algae, the grazers press brushes, rakes, gouges, excavators, or rasps against the rough surface of the stones and move these tools back and forth. During such a mode of working, strong abrasion of the mouthparts is unavoidable. In addition to the progressive destruction of the tools used for detaching the food, significant defects also occur on the grinding structures of alga grazers.

The phenomenon of natural wear of the feeding apparatus of arthropods has been observed in only a few cases to date (e.g., Williams 1954; Edwards 1980; Rausher 1981; Raupp 1985; Currie and Craig 1987). Mouthpart defects have usually been overlooked or misdiagnosed by taxonomists and morphologists because the mouthparts have been examined from the wrong perspective. Specifically, their functional aspects have often been insufficiently considered. For example, in their excellent study on the larval head of Blephariceridae, Anthon and Lyneborg (1968) described two types of mandibles in *Liponeura* and tried to attribute these to different larval stages. However, in one case they drew an unused mandible, and in the other an extremely worn mandible of the same stage. Nielsen (1942) suggested that the shortening of the mandibles of *Agapetus* takes place during the construction of the pupal case, although he previously characterized this caddisfly larva as an alga grazer scraping rough stones with its mandibles.

Thus, the wearing down of mouthparts is a theme not treated in detail until now. Because of their specific mode of harvesting food, alga grazers in streams are suitable subjects for demonstrating that wear and tear of feeding apparatus is an important adaptational problem. Theoretically, there are three possible ways of solving this problem: (*i*) reduction of the deterioration rate; (*ii*) specific construction or use of the scraping organs so that only extreme wear causes diminished efficiency; and (*iii*) replacement of worn structures by undamaged ones. To determine which of these three adaptations has actually evolved,

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alga grazers from a wide range of taxa (Insecta, Crustacea, Gastropoda, and Pisces) were chosen and investigated comparatively by scanning electron microscopy (SEM). In addition, laboratory experiments were used to establish whether the degree of roughness of the substratum is correlated with the amount of abrasion of the scraping apparatus, and whether wearing defects induce premature ecdysis in ephemeropteran larvae.

Morphological comparison of very different alga grazers provides the basis for a discussion of the extent to which the morphological ground plan of a taxon determines or excludes specific solutions to the problem of wear and tear.

Materials and methods

Study animals

Specimens of the following genera were gathered near Freiburg, Federal Republic of Germany, in streams of the Black Forest mountains: *Rhithrogena* and *Epeorus* (Ephemeroptera: Heptageniidae), *Baetis* (Ephemeroptera: Baetidae), *Ameletus* (Ephemeroptera: Siphlonuridae), *Brachyptera* (Plecoptera: Taeniopterygidae), *Glossosoma* (Trichoptera: Glossosomatidae), *Limnius* (Coleoptera: Elmidae), *Liponeura* (Diptera: Blephariceridae), and *Ancylus* (Gastropoda: Basommatophora).

Lepeorus goyi (Leptophlebiidae), a grazing mayfly larva dwelling in streams of New Caledonia, was obtained from the Museum of Natural History of Vienna. Dipteran larvae of the genus *Oxycera* (Stratiomyidae) were collected from river sources near Savognin (Canton of Graubünden, Switzerland), and *Ligia italica* on rocky shores near Catania (Sicily). This marine isopod was chosen for this study because grazing crustaceans are not found in European streams. It detaches epilithic algae from stones exposed to the tide. Specimens of *Garra taeniata*, a tropical cyprinid, were obtained from aquarist shops. Other than these fish, all investigated animals had previously fed only in their natural habitat.

With the exception of the riffle beetle *Limnius*, only larval stages of named insect species were analyzed. I generally chose larvae at a later stage of development because another (more detritivorous) feeding mode might be expected in younger larvae of some taxa (e.g., Ephemeroptera, Plecoptera). At least 10 specimens of each species were examined by SEM, and many other individuals were inspected by light microscopy. The mouthparts of most showed moderate wear. Completely undamaged structures were found in only a few larvae, most of which were freshly moulted. Extreme wear occurs more frequently in the last instars.

Preparation

For SEM the mouthparts were dissected out, fixed in ethanol, and dehydrated (critical point apparatus model 020, Balzers, Liechtenstein). The preparations were coated with gold (Sputter E 5100, Polaron, München) and examined with a scanning electron microscope (Nanolab 7, Zeiss). Mouthparts of the alga grazers were sometimes cleaned; this was always performed mechanically by means of a fine hair pencil and a syringe. Chemicals or ultrasonic techniques were never used.

Laboratory experiments

Ephemeropteran larvae were kept in a laboratory stream at 12°C. They grazed on either smooth clay discs or pieces of water-resistant sandpaper mounted on clay discs. Both types of substratum were coated with a thin uniform layer of algae (sedimentation method, Bohle 1978); algal coatings on stones in streams were brushed off and then suspended in a tub. The algae, sand particles, and other components of the natural algal pastures sank onto the clay discs and pieces of sandpaper (3 cm diameter) at the bottom of the tub. Two days later, the deposited algae had anchored themselves to the discs. However, they were not very tightly attached to the substratum, so they could be more easily grazed than natural algal pastures. Under these circumstances, the wear on the animals' mouthparts would be less than in natural conditions. The coated substratum discs were stored in a freezer at −20°C.

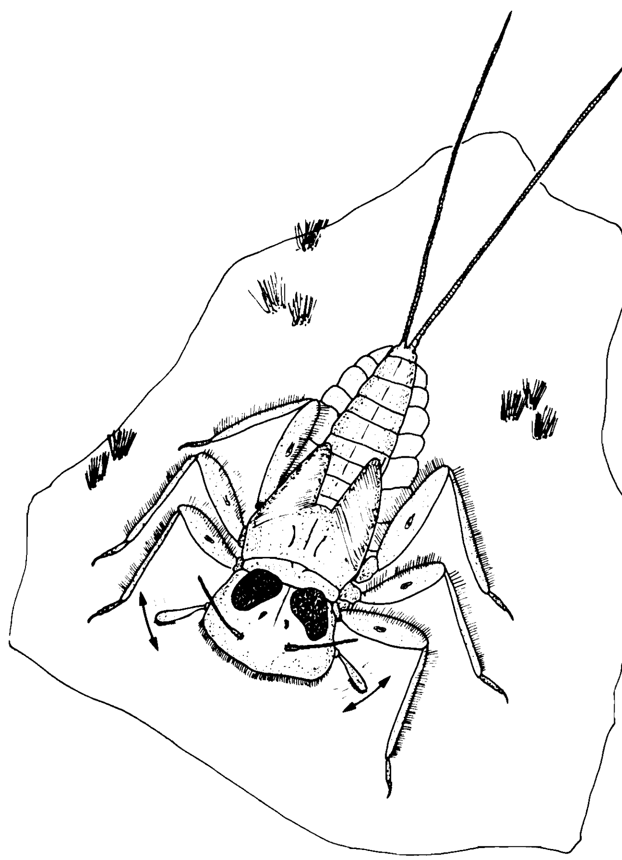


FIG. 1. The mayfly larva *Epeorus* grazing on an epilithic algal pasture. The arrows show the movements of the maxillary palps.

Only one larva was put into each vessel in the laboratory stream. The food was not limited. I monitored daily which substratum discs had been grazed out and must be replaced and whether the larva had moulted. Discs not grazed out after 3 days were removed.

Results

For gathering and ingesting food, alga grazers use a set of complex mouthparts that work in close cooperation: a scraping apparatus removes the algae from the stone, different collecting organs transport the food towards the mouth, and crushers open the algal cells before they are digested. A comparative description and functional analysis of these mouthparts is given by Arens (1989) for 25 species from different taxa; single species have been examined in detail by Schremmer (1951*a*, 1951*b*), Strenger (1953), Schönmann (1981), McShaffrey and McCafferty (1986, 1988), and other authors. In the present study, I will show that the scrapers and crushers of alga grazers become worn down during use. The collecting organs are not included in this study because they are not subject to wear.

Wear of scraping apparatus

Wearing defects of scraping apparatus can usually be observed in alga grazers, and occur in all taxa. The wearing down of mouthparts is such a common phenomenon in this animal community that specimens without defects can rarely be found in their natural habitat. Figures 2–15 offer an impression of which kinds of defects occur and to what extent scrapers become worn down under natural conditions. Wearing down is always a gradual and continuous process. If drastic damage such as breakage takes place, the breaks occur only in the fine structures of the apparatus. This applies to all five types of tools that are suitable for detaching epilithic algae (Arens 1989): brushes (Figs. 2–4), rakes (Figs. 5–8), gouges (Figs. 9–12), excavators (Figs. 13–14), and rasps (Figs. 15–16).

The micrographs speak for themselves; the wearing down of the organs while scraping on rough stones is so extensive that the functionally important structures are totally destroyed (e.g., Figs. 2, 3, and 9). However, the type and degree of deterioration differ from species to species. The pertinent examples are arranged according to the type of scraper used by the animal.

Alga grazers that use brushes

Brushes are composed of a large number of slender, bristle-like fine structures which are arranged in clusters on the ventral side of one or more pairs of mouthparts.

Epeorus and *Rhithrogena*: Nearly all mayfly larvae of the family Heptageniidae (Fig. 1) use their two-segmented, strongly modified labial palps as alga scrapers. The distal palpal segment is ventrally equipped with a large brush composed of transverse rows of sickle-shaped bristles (Figs. 2*a* and 2*b*) which are considerably worn down while scrubbing across the substratum. The larvae press their brushes at an angle against the substratum, so that at first only the bristles along the front of the brush lose their tips (Fig. 2*c*). As the brush wears down from front to back, it must be lowered a little farther so that unused bristles are put into action. The brush "works itself in" (see also Fig. 8). In the case of extreme wear, the anterior bristles disappear completely, even the integument in this region being abraded (Fig. 2*d*).

In *Rhithrogena* and some other genera such as *Epeorus*, the maxillary palps also carry large scrubbing brushes on the ventral side of the distal segment (Fig. 3*a*). The fine structures of these brushes are comb bristles (Fig. 3*b*). During their 1- to 2-week period of use, these bristles successively lose their curved prongs (Figs. 3*c* and 3*d*); some become so worn down that only small stubs remain (Fig. 3*e*).

Limnius: The riffle beetle *Limnius* detaches epilithic algal layers by means of brushes on the distal part of its laciniae (Fig. 4*a*). The brushes consist of three rows of robust, sickle-shaped bristles whose curved tips can disappear as a result of intensive wear (Fig. 4*b*). More extensive wear defects were never found in this species.

Alga grazers that use rakes

A rake is formed by a single row of relatively solid prongs and is usually positioned along the distal edges of the mouthparts.

Ameletus inopinatus: The larvae of several mayfly families have a row of flexibly mounted comb bristles along the ventrodistal edge of their maxillae. In most ephemeropteran larvae, these structures form a detritus broom or cleaning apparatus. The comb bristles of *Ameletus*, however, are fused secondarily with the integument and serve as prongs of an alga rake (Fig. 5*a*). The typical sign of wear on this apparatus is breakage of the comb prongs; an extremely deteriorated rake consists of a row of nearly smooth bars (Figs. 5*b* and 5*c*). Complete loss of comb bristles is rarely found, but can occur (see left margin of Fig. 5*b*).

Oxycera: The mouthparts of *Oxycera* and other stratiomyid larvae are strongly modified. The labrum and the labium together form a vertical wall which divides the preoral cavity into two compartments. A pair of two-segmented mandibular–maxillary complexes, fusion products of the mandibles and maxillae (Bischoff 1925; Schremmer 1951*a*, 1951*b*; Rozkosny 1982), swings backwards and forwards along both sides of this separating wall; they can also grasp food. In *Oxycera* larvae, the distal segment of these mandibular–maxillary complexes is ventrally equipped with three rakes of different degrees of coarseness (Fig. 7). The first rake is composed of very coarse cuticular structures (Fig. 6*a*); it probably functions only as a scraper. The other rakes are both more distally placed, and their sickle-like prongs (Figs. 7 and 8) appear to be well suited for collecting and sweeping the algal material loosened by the coarse rake.

The *Oxycera* larvae examined had grazed on algal pastures attached to very rough stones. Nevertheless, signs of extensive wear were found only on the coarse first rake of their mandibular–maxillary complexes: the hooks of a moderately deteriorated rake are cut down and have rounded tips (Fig. 6*b*). The upper layers of the cuticle delaminate in an extremely worn apparatus (Fig. 6*c*). The second rake also becomes worn down, but the degree of wear is insignificant; the distal part of some sickle-shaped bristles is abraded (Fig. 8), indicating that these prongs had made contact with the rough substratum. The fine third rake, which probably functions only as broom, never deteriorates to an appreciable extent.

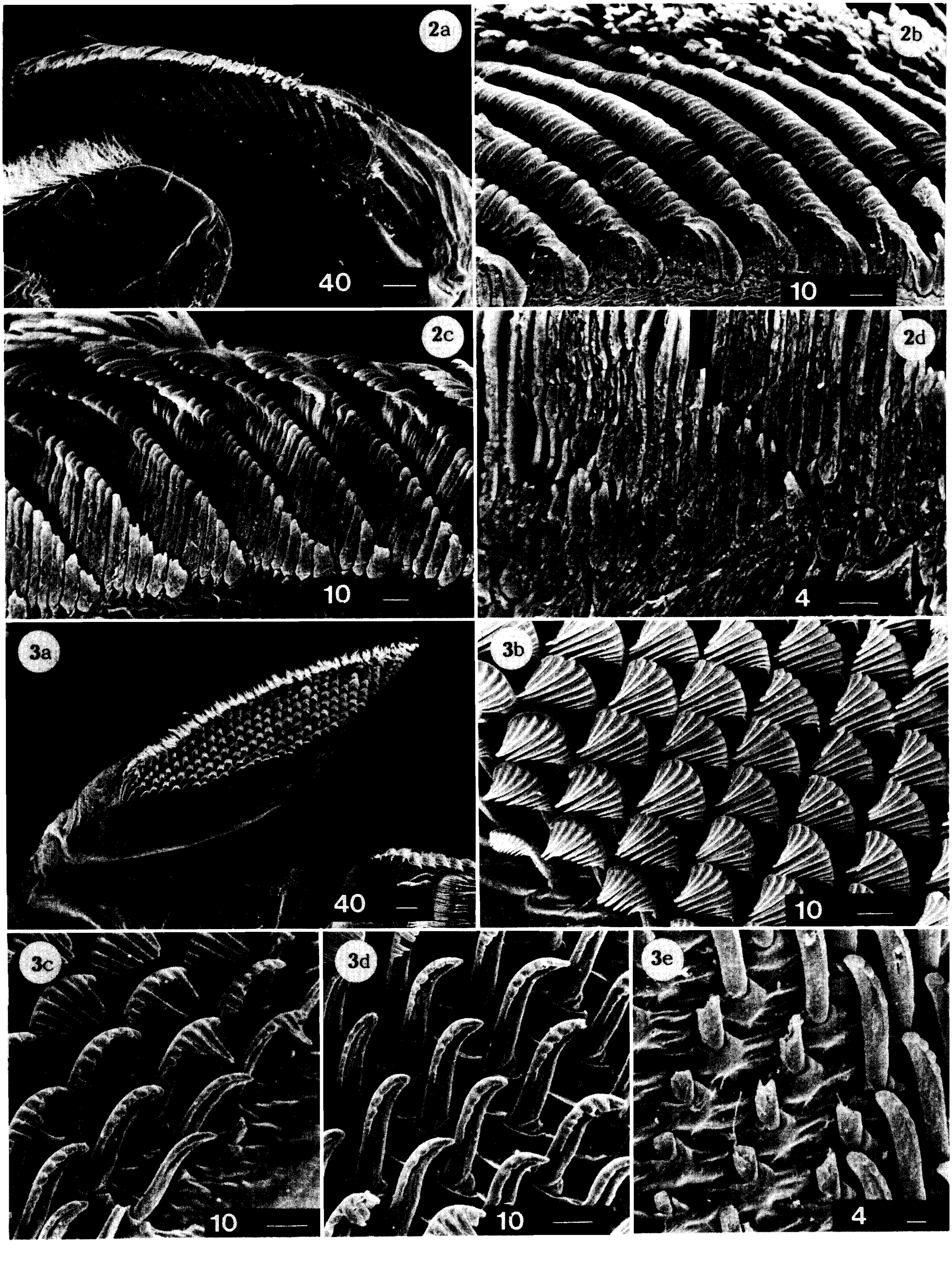
Alga grazers that use gouges

The gouge is the most common type of scraping apparatus found among alga grazers. It is characterized by a shovel-like blade distally equipped with a sharp cutting edge. Gouges usually become considerably worn down when used on rough stones. Four examples of animals from different taxa demonstrate the extent of wear defects.

Baetis: This mayfly larva grazes on algal layers by using its gouge-shaped mandibular tips as scrapers. The dark-coloured and heavily sclerotized blade of an unused gouge has dentate edges and is much longer than the comb-like lacinia mobilis (Figs. 9*a* and 9*c*). In the course of continued deterioration, the blade abrades so extensively that its final length is only one-third of the original length (Figs. 9*b* and 9*d*). Despite this extensive wear, however, the functionally important cutting edge of the gouge is sharp at all stages of abrasion (Figs. 9*d* and 9*e*). The cuticle of the gouge blade is obviously composed of two or more layers that have a different structure and hardness. The upper layer of the cuticle contains longitudinal fibres and is worn more rapidly than the lower layer, which consists of a nonfibrous material (Fig. 9*e*). The consequence of this anatomy is the self-sharpening of the gouge during its use.

When abrasion has progressed to the pale-coloured basal part of the gouge, the signs of wear of the cuticle change and indicate that in this region the fibrous layer is much thinner or even absent (Fig. 9*d*). In my test specimens, abrasion never penetrated the cuticle to the hypodermis. Even if this should happen, development of the mouthparts of the next instar would

Scale bars in Figs. 2–6 and 8–22 are in micrometres. FIG. 2. Labial palpal brush of *Epeorus*. (*a*) Ventral side of the left terminal palpal segment equipped with a scraping brush. (*b*) Fine structures of an unused brush. (*c*) A brush showing moderate defects arising from wear. (*d*) Extremely abraded, sickle-shaped bristles. Note the direction of the scratches which indicates the course of the scraping movement of the palp. FIG. 3. Scraping brush on the maxillary palp of *Rhithrogena*. (*a*) Ventral side of the terminal segment of the right palp. (*b*) Intact fine structures. (*c*) Moderately worn comb bristles. (*d*) Very worn comb bristles. (*e*) Extremely worn bristles.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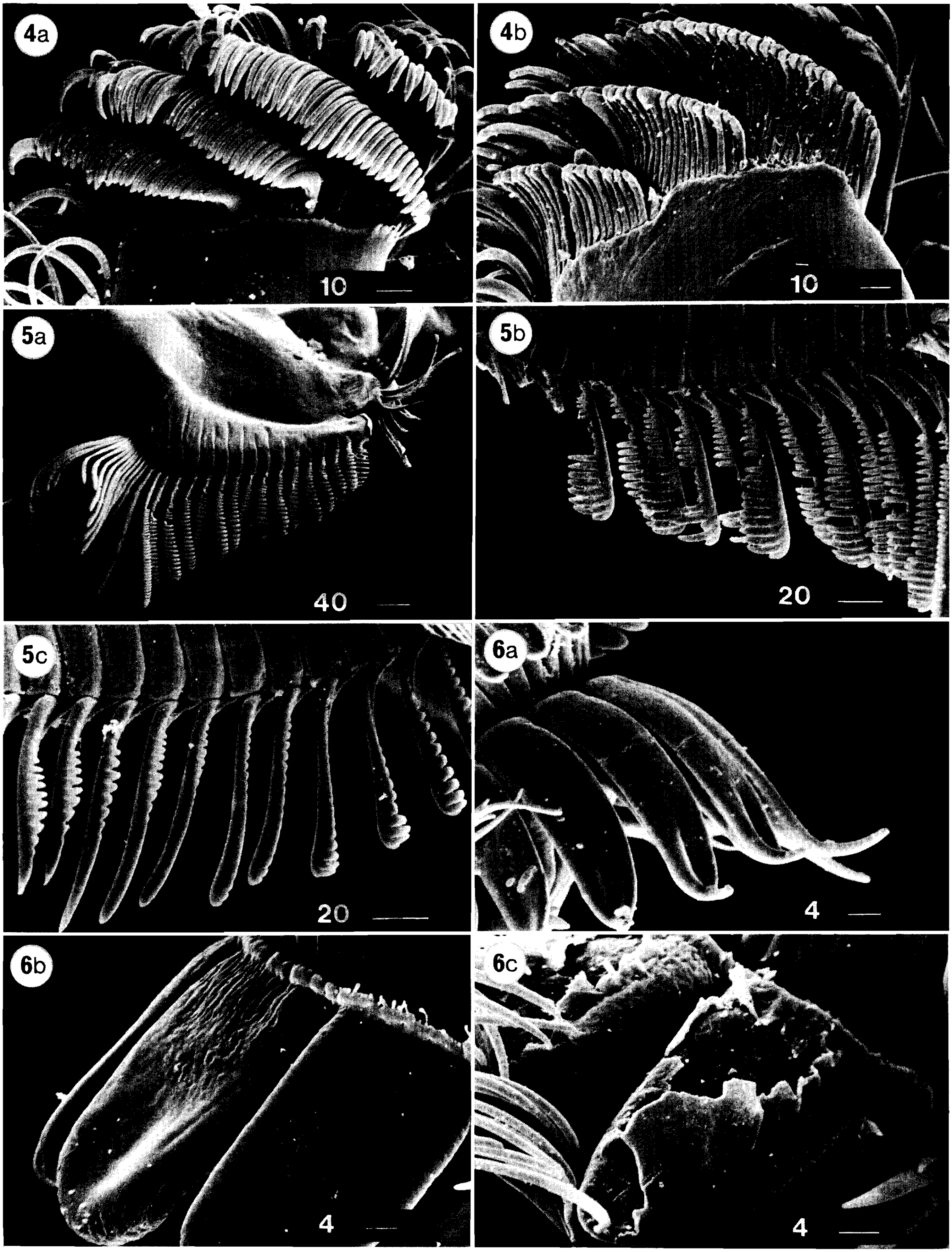


FIG. 4. *Limnius*, scraping brush on the tip of its lacinia. (*a*) Unused apparatus. (*b*) Strongly abraded brush. FIG. 5. *Ameletus*, rake along the distal edge of the maxilla. (*a*) Intact apparatus (frontal view of the maxilla). (*b*) Very worn apparatus. (*c*) Extremely worn apparatus. FIG. 6. *Oxycera*, coarse rake on the mandibular–maxillary complex. (*a*) Well-formed rake of a freshly moulted larva. (*b*) Moderately worn rake. (*c*) Delamination of a cuticular layer resulting from marked abrasion.

not be impaired, as the new organs are not formed directly under the old cuticle. Furthermore, feeding activity decreases near the end of a moulting interval during which the new organs develop.

Brachyptera: The stonefly larvae of the genus *Brachyptera* have two pairs of maxillary scraping apparatus: brushes on the ventral side of the galeae and the gougelike distal parts of the laciniae. Both types of apparatus become considerably worn down. Figure 10*a* shows the gouge on the lacinia of a freshly moulted *Brachyptera* larva and Fig. 10*b* shows the same apparatus after it has been severely abraded. Fibrous disintegration of the cuticle resulting from abrasion never occurred in this species.

Agapetus: *Agapetus* and other glossosomatid caddisfly larvae are highly specialized grazers that use their mandibles to remove algae from stones. All parts of their mandibles are black and heavily sclerotized. The very long (ca. 150 μm in larva V) gouge blade of the mandibles can be lost because of abrasion during a moulting interval (Figs. 11*a* and 11*b*). The signs of wear on the blade are similar to those described earlier for *Baetis*. However, a fibrous cuticular layer is found not only on the upper side of the *Agapetus* gouge (Fig. 11*c*) but also on the lower side (Fig. 11*d*). The cuticle of the basal part of the blade obviously has the same microanatomy as that of the distal part.

Ligia: In this marine isopod, the incisor cusps of the mandibles form a gouge (Fig. 12*a*). Although *Ligia* usually has to remove its food from very rough rocks, the abrasion of its scraping apparatus is less extensive than in most grazing insects (Fig. 12*b*). The typical sign of wear on the *Ligia* mandible is the breakage of some cuticular pieces from the gouge blade. The cutting edge of a worn gouge is therefore notched.

Alga grazers that use excavators

Functionally, the most important part of excavators of stream-dwelling grazers is a large scoop which is either composed of robust prongs or formed by a concave plate. Sometimes several excavators work in series, in a similar manner to a rotary bucket excavator.

Ligia italica: In addition to the gouge-shaped mandibular tips, an excavator on the end of the first maxillae is used by the isopod *Ligia* for grasping food. Five long hooks are arranged in a semicircle on the most distal part of the maxillae, where they form a shovel (Fig. 13*a*). A group of smaller comb bristles inserted beneath this shovel may represent a cleaning apparatus that sweeps collected food towards the mouth across fields of hairs on the second maxillae (Arens 1989). A similar function is probably carried out by a long single bristle which is distally equipped with a tassel and projects into the concavity of the shovel.

Signs of wear indicate that both the shovel and the comb bristles make contact with the rough rocks when *Ligia* detaches food from this substratum. After strong abrasion, both types of structures lose their distal part (Fig. 13*b*). The prongs of the comb bristles disappear. The tasseled bristle, however, is normally not worn down, probably because of its long, elastic shaft.

Liponeura: Like most other dipteran larvae (cf. *Oxycera*), the blephariceridid larva *Liponeura* has mandibles that do not move vertically inside the preoral cavity, but swing parallel to each other backwards and forwards. A wall formed from the labrum and labium separates them, whereas the greatly modified maxillae serve as lateral barriers in the preoral cavity against the current (Anthon and Lyneborg 1968; Arens 1989). In the last instar, the mandibles of *Liponeura* are equipped with two large shovels which are slightly domed; they scrape across the substratum with their distal edge. The shape of an extremely

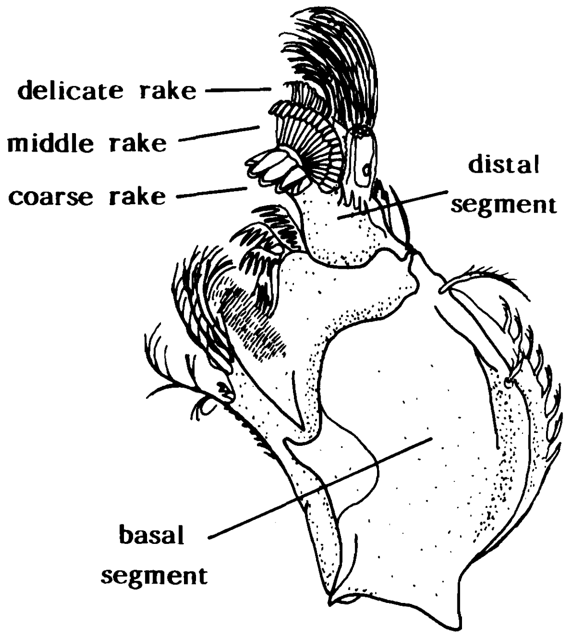


FIG. 7. *Oxycera*, inner face of the right mandibular–maxillary complex equipped with scraping rakes (from Schremmer 1951*a*).

worn mandible differs considerably from that of a new organ, since abrasion results in a marked shortening of the shovels (Fig. 14; see the Introduction). As described earlier for the gouge of *Baetis*, the shovels of *Liponeura* always stay sharp because of the microanatomy of the cuticle. However, instead of one fibrous layer above the cutting edge there are several cuticular layers, some having a dense structure and others being very porous (Figs. 14*d* and 14*e*).

Alga grazers that use rasps

The rasps of alga grazers have relatively short and sturdy structures compared with the hairs and bristles of scraping brushes. Rasps have often evolved in larger grazers but obviously not in arthropods (Arens 1989).

Ancylus: The limpet *Ancylus* is the only European snail that feeds on algal layers on stones in fast-running streams. Its radula is a long chitinous band studded with numerous transverse rows of curved teeth. This organ functions as a rasp. When the snail presses the distal region of its radula against the substratum and draws the organ back, the teeth remove food from the stone and transport it into the mouth. The rasp structures on this distal region that scrapes across the rough substratum always show signs of considerable wear (Fig. 15). All teeth more centrally positioned within a transverse row are considerably abraded and lose their curved, notched tip. However, abrasion also occurs on the marginal teeth, each of which is divided into a small comb-shaped part and a hook-like structure (Arens 1989).

Garra taeniata: The cyprinid fish *Garra taeniata* inhabits streams in Southeast Asia and is specialized for grazing on algae that grow on water plants and stones. Its feeding organ is a horny layer coating both jaws. The surface of this horny lamella is densely studded with small, shingle-like projections that together form an effective rasp. Similar jaw equipment is present in *Labeo bicolor* and some other grazing fish (Arens 1989). I have no information about the wear of this rasp under natural conditions because the fish in this study were reared in tropical fish hatcheries and were bought in aquarist shops. However, the degree of deterioration seems to be similar to that observed in other grazers, the consequence being abrasion of the rasp structures. Occasionally, *G. taeniata* sheds the horny rasp coat, thereby uncovering a fully developed replacement (Fig. 16). This "moulting" of the grazing organ results in the renewal of an old (worn) apparatus.

Abrasion of grinding apparatus

The food of alga grazers is a mixture of diatoms, other single-celled algae, detritus, and grains of sand. Diatoms have hard silicious shells, and green algae are protected by a solid cellulose wall, so many grazers cannot digest harvested algae before they have been cracked or mechanically torn open (Neumann 1961; Winterbourn 1971). Therefore, most grazers must have some form of grinding apparatus (Arens 1989). In grazing aquatic insects, molar surfaces on the mandibles are the most common type of crusher, whereas effective proventriculi or other grinding organs in the gut occur only in few taxa. The following examples will show that the fine structure of mandibular molar surfaces and of crushers in the gut of insects are considerably worn down by grinding the ingested mixture of algae and sand.

Mandibular molar surfaces

The pars molaris of the mandibles is usually well developed in grazing insects. Three types of mandibular molar surfaces equipped with characteristic fine structures have evolved at different times, with striking convergence among these animals: the thorn-carpet molar surface which is densely studded with sharp spines, the ridge-studded molar surface over which several transverse masticatory ridges run, and the grating-like molar surface which is also equipped with ridges but has crossbars between these ridges (Arens 1989). When the mandibles swing in, their molar surfaces press and grind food particles enclosed between them. Typical wear of these crushers takes the form of abrasion and smoothing of the protrusions on their grinding surface; as a result of chewing movements, the sharp thorns of the thorn-carpet molar surface are blunted or even, after extensive use, cut down (Fig. 17). Small granules on the masticatory ridges completely disappear following the grinding of hard food (Fig. 20). Indeed, the abraded top of the ridges is leveled and extensively scratched. However, not only delicate granules but also solid humps (Fig. 19) and protruding parts of gratings become worn down (Fig. 18). On the other hand, the main masticatory structures (e.g., gratings or ridges) were never completely lost in any of the species studied.

The pharyngial mortar of Oxycera

Many stratiomyid larvae crush detached algal food by means of a heavily sclerotized mortar formed from the distal section of the pharynx (Schremmer 1951*a*, 1951*b*; Arens 1989). In *Oxycera* the floor of the pharynx forms a mortar, and its roof produces a large grinding tooth that swings backwards and forwards in the shell (Fig. 21). The margins of the tooth and the posterior half of the shell are equipped with transverse masticatory ridges (Fig. 21*b*). The structures of this mortar get worn down much more extensively than the mandibular molar surfaces described earlier. A moderately worn grinding tooth has smooth ridges because its small granules have been abraded (Fig. 21*c*). After extreme abrasion, however, the complete apparatus, with its masticatory ridges, is lost (Fig. 21*d*). The ridges are abraded to such an extent that their hollow interior is exposed and only rudiments of the deep furrows between them are left along the margins of the tooth. The grinding tooth of the next instar develops elsewhere in the head, so that it cannot be damaged before moulting, even if the cuticle of the old tooth is penetrated as a result of strong abrasion.

The extent of wear found in the mortar is similar to that of the grinding tooth.

Experiments on the correlation between the degree of wear of mouthparts and the roughness of the substratum

Mayfly larvae of the genus *Epeorus* wear down their palpal brushes only if they have to detach epilithic algae from rough surfaces. When the larvae scrape on smooth clay discs, their palpal brushes remain almost undamaged for a whole moulting interval.

Figure 22*a* shows the scraping brush of a larva that had previously grazed for one moulting interval (11 days) on an algal pasture attached to a smooth substratum. Damage resulting from wear is minimal and only discernible at higher magnification (Fig. 22*c*). Only a few sickle bristles have lost their tip. The cuticle in front of the brush is completely undamaged (Fig. 22*e*). The micrographs were obtained during SEM examination of the exuvia.

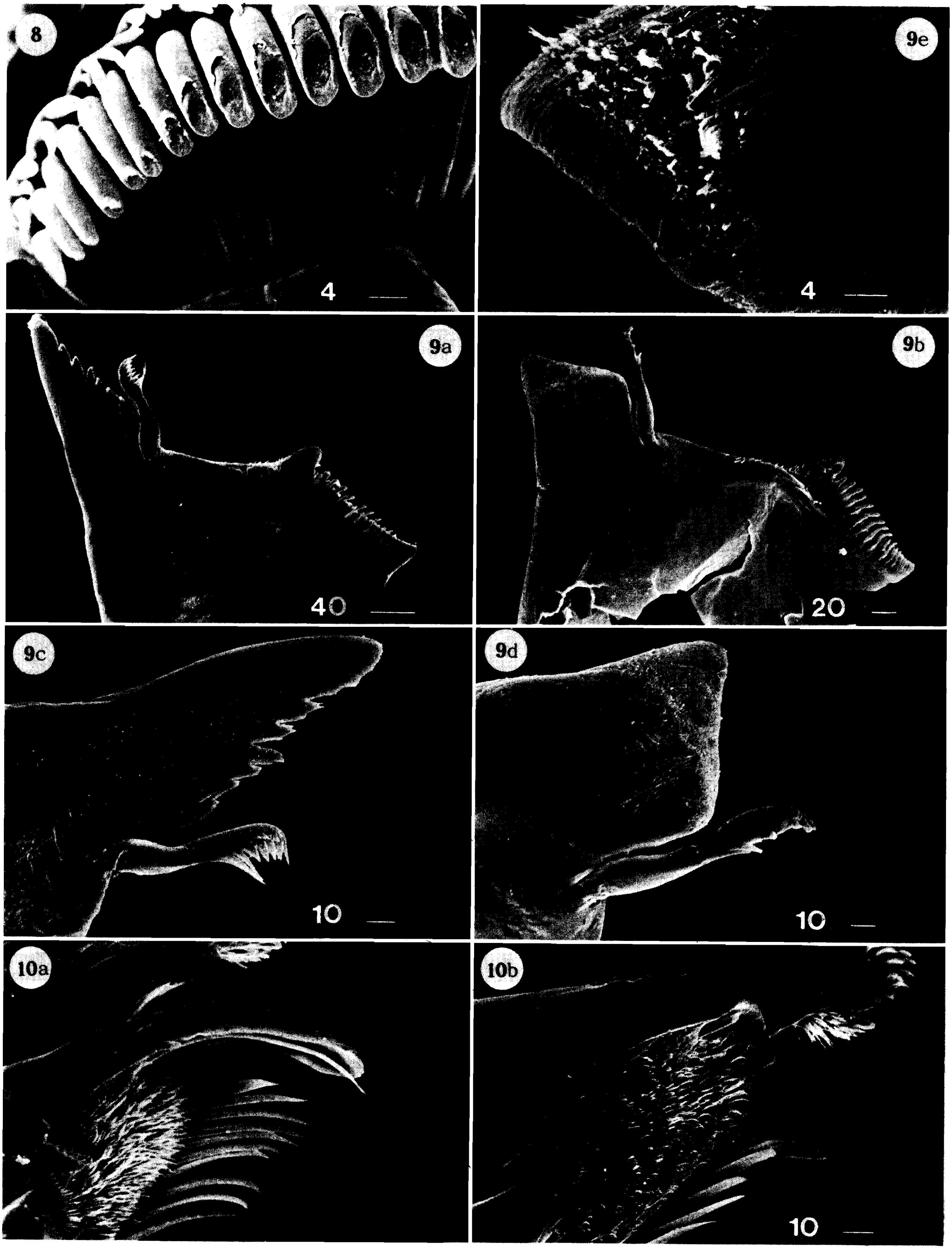
After the larva had moulted, it was placed on grade 280 sandpaper coated with the same algal layer as described earlier. During the following 12 days, until the next ecdysis, the palpal brushes became considerably worn down (Fig. 22*b*) as a result of their being used to scrape the rough substratum. Their wear defects were similar to those of larvae that had grazed under natural conditions (cf. Fig. 2*c*): the bristles of the anterior part of the brush were abraded (Fig. 22*d*), and moreover, the integument in front of the brush was extensively scratched (Fig. 22*f*). Obviously this part of the brush had come into contact with the sharp, pointed particles on the sandpaper. All other test specimens (five) that I examined by SEM showed very similar signs of wear caused by the sandpaper, but had almost undamaged mouthparts after scraping smooth clay discs.

In both cases, on the clay discs and on the sand paper, the larvae grazed down the algal layers completely. When the larvae had to remove algal layers from sandpaper, not only the scraping brushes of the labial palps deteriorated but also those of the maxillary palps. During feeding on a smooth substratum the scraping structures remained almost undamaged. On the other hand, the molar surfaces of the mandibles wore down under both test conditions, irrespective of the nature of the substratum.

Experiments to test whether wear damage to mouthparts induces ecdysis

Epeorus larvae were examined in the laboratory to test whether damage from wear influences the frequency of ecdyses. At first, all larvae grazed on smooth clay discs which had been coated with algae. After the second ecdysis in the laboratory stream, I divided them into three groups. Larvae of the first group (A) continued to feed on the smooth substratum. Larvae of the other two groups (B and C) were placed on sandpaper (grade 400 or 280); they then wore down their mouthparts by

FIG. 8. *Oxycera*, middle rake of the mandibular–maxillary complex, extremely worn. The defects show clearly which bristles make contact with the rough substratum. FIG. 9. *Baetis*, left mandible with gougelike tip, dorsal view. (*a*) Unused gouge. (*b*) Extremely abraded mandible. (*c*) Cutting edge of an unused gouge. (*d*) Cutting edge of an extremely deteriorated gouge. (*e*) Distal part of an abraded gouge. Note the disintegration of the cuticle into fibres and the smooth, sharp cutting edge. FIG. 10. *Brachyptera*, showing wear on the maxillary gouge. (*a*) Unused apparatus. (*b*) Extremely abraded apparatus.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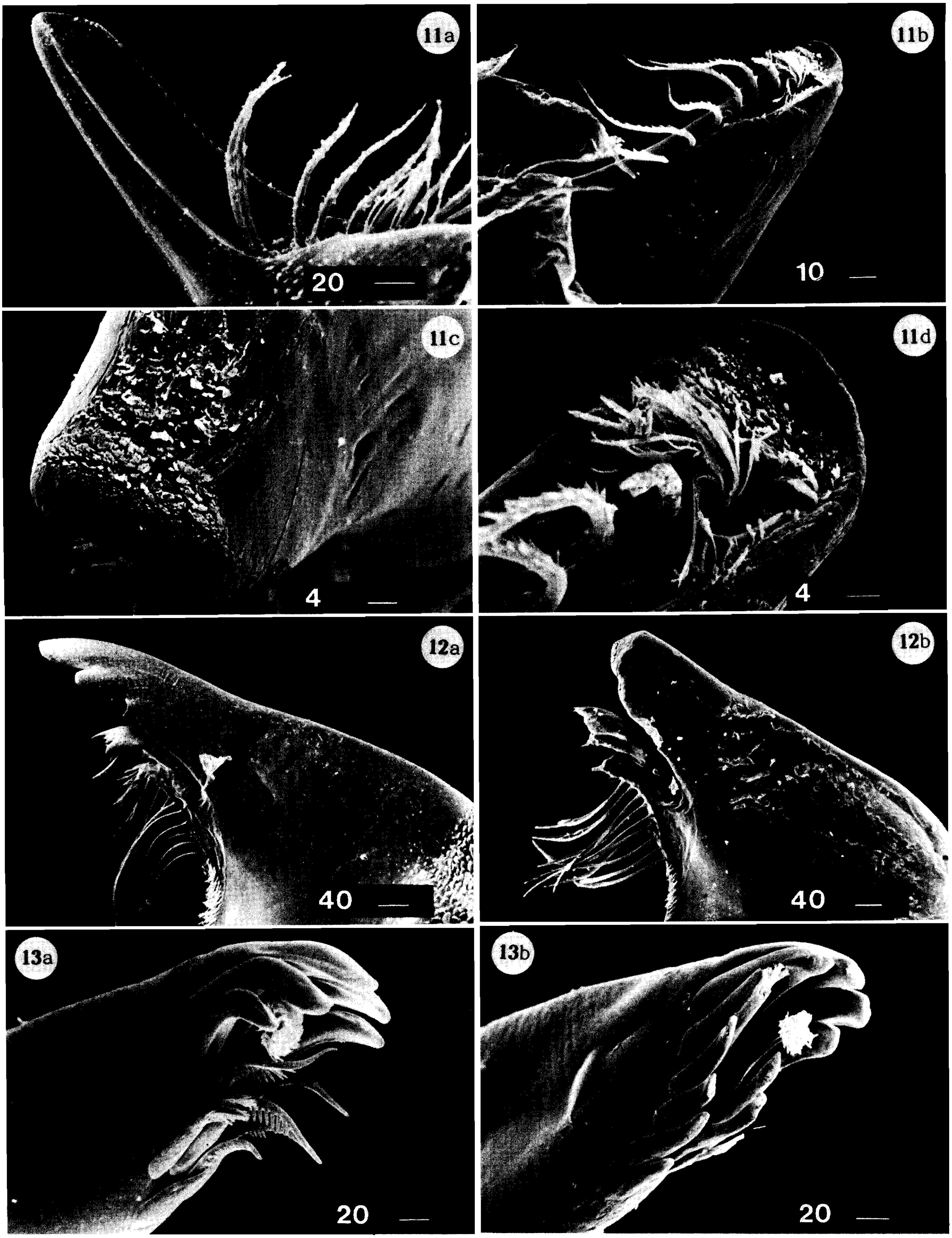


FIG. 11. Glossosomatidae, showing wear defects on the mandibular gouge. (*a*) Almost unused right mandible. (*b*) Extremely deteriorated gouge. (*c* and *d*) distal part of an abraded gouge, dorsal (*c*) and ventral (*d*) views. Note the smooth, sharp cutting edge and the fibrous disintegration of the cuticle. FIG. 12. *Ligia*, showing wear on the gougelike mandibular tip. (*a*) Intact apparatus. (*b*) Extremely abraded apparatus. FIG. 13. *Ligia*, showing wear on the excavator at the tip of the first maxilla. (*a*) Unused apparatus. (*b*) Apparatus with deteriorated fine structures.

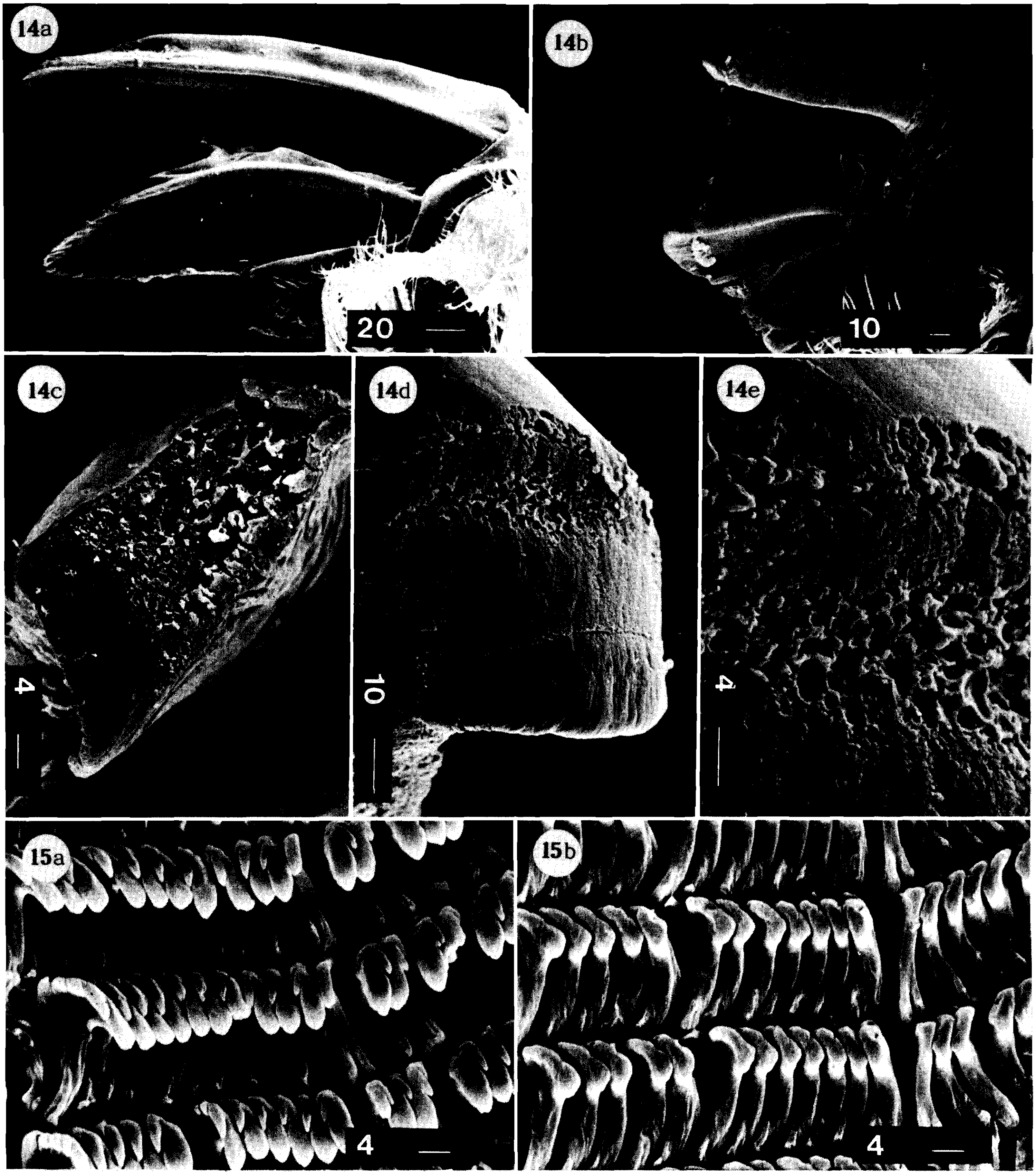


FIG. 14. *Liponeura*, showing deterioration of the mandible. (*a*) Mandible of a freshly moulted larva (fourth instar). (*b*) Extremely abraded mandible (fourth instar). (*c*) Exterior surface of a worn mandibular blade. Note the sharp, smooth cutting edge. (*d* and *e*) Exterior surface of an extremely worn blade, oblique lateral view. Note the different cuticular layers seen on the abraded surface of the stub of the excavator. FIG. 15. *Ancylus fluviatilis*, showing abrasion of the radula. (*a*) Unused teeth near the radula's central line. (*b*) Strongly abraded radula teeth.

scraping on this rough substratum (see experiment described earlier). The mortality of the larvae in the laboratory stream was high; most of them died within the first month, after having been infected by fungi. Only specimens that had moulted at least 3 times in the laboratory were taken into consideration. Table 1 shows the moulting intervals of these larvae before and after they were divided into the three groups. Only specimens that had moulted at least 3 times in the laboratory are included.

No distinct shortening of the main moulting intervals is noticeable as a consequence of moving larvae from a smooth to a rough substratum. Some larvae in groups B and C spent a longer time between ecdyses than others. However, similar variations in moulting intervals also occur in group A and are obviously normal. The data presented provide no evidence that mayfly larvae shorten their moulting intervals after their mouthparts have worn down. If a correlation exists between the amount of

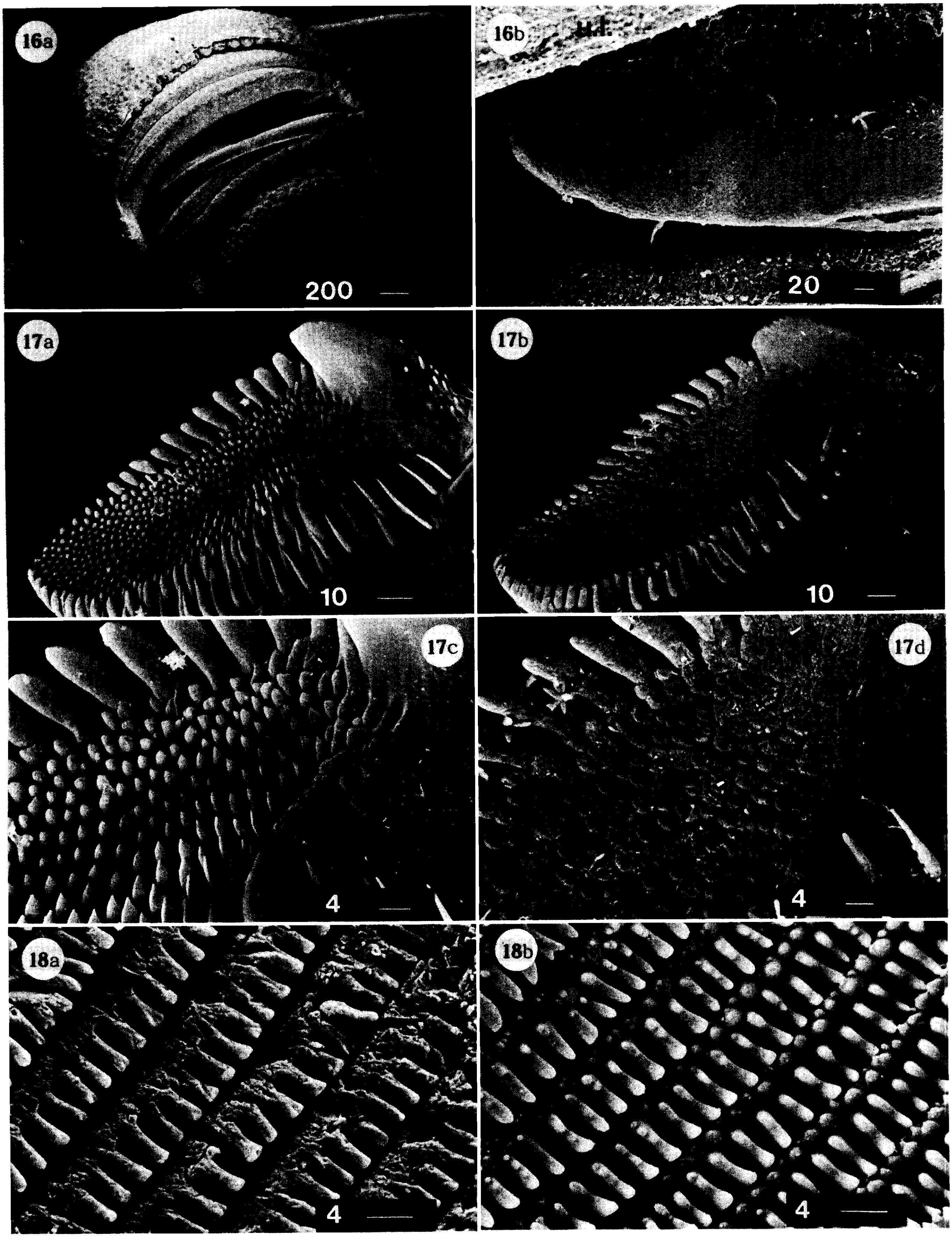


FIG. 16. *Garra taeniata*, showing moulting of the horny rasp coat of the jaws. (*a*) Horny coat of the lower jaw during delamination. (*b*) Lateral part of the delaminated horny rasp (*d.r.*) at higher magnification. Note the new rasping apparatus (*n.r.*) situated below it. *u.l.*, upper lip. FIG. 17. *Baetis*, showing worn down mandibular molar surface. (*a* and *c*) Molar surface of the left mandible, unused. (*b* and *d*) Same apparatus, markedly worn down. FIG. 18. *Epeorus*, showing fine structures on the molar surface, (*a*) unused, and (*b*) considerably deteriorated.

TABLE 1. Moulting frequency (number of days between ecdyses) of 23 *Epeorus* larvae feeding on substrata of different degrees of roughness

Group A[a]

Larva No.	On smooth substratum												
1	11	11	12	13									
2	11	11	12	12	17								
3	11	10	11	13	12	14	13						
4	12	13	11	9	12	12	11						
5	16	20	8	14	14	14	12	13	14	15			
6	10	10	11	9	11	11	10	12	16	13	11	16	15
Mean	11.8	12.5	10.8	11.7	13.2	12.8	11.5	12.5	15.0	14.0	11.0	16.0	15.0
SD	2.14	3.83	1.47	2.16	2.39	1.50	1.29						

Group B[b]

Larva No.	On smooth substratum		On sandpaper, grade 400					
7	10	10	13					
8	10	11	15	10				
9	17	15	13	15				
10	10	10	13	15				
11	11	10	11	12	13	13		
12	11	14	9	12	15	15		
13	14	11	11	11	12	13	13	17
14	11	13	11	10	11	12	12	14
Mean	11.8	11.8	12.0	12.1	12.8	13.3	12.5	15.5
SD	2.50	1.98	1.85	2.12	1.71	1.26		

Group C[b]

Larva No.	On smooth substratum		On sandpaper, grade 280				
15	11	12	16				
16	8	12	13				
17	9	13	11				
18	10	11	12	11			
19	10	13	11	15	15	15	
20	11	11	12	10	16	15	
21	9	8	10	13	9	16	9
22	8	10	12	13	9	9	9
23	10	8	10	9	8	13	12
Mean	9.6	10.9	11.9	11.8	11.4	13.4	10.0
SD	1.13	1.90	1.83	2.23	3.78	2.79	

[a]Larvae scraped smooth clay discs for the duration of the experiment.
[b]After two ecdyses, the smooth substratum was exchanged for sandpaper.

wear of the brushes and the frequency of ecdyses, it is not significant.

Discussion

Stream-dwelling alga grazers are a very interesting animal community to use for investigations concerning the evolution of complex mouthparts and their adaptation to a highly specialized feeding mode. The food of these animals, epilithic algal layers, is present in all streams in large amounts. Furthermore, the algal pastures are available throughout the year and regenerate swiftly after they have been overgrazed. Because of the richness of this food source, a great variety of animals have independently acquired the ability to graze algal pastures.

Various species of these alga grazers now live together in the same streams, on the same stones. All these species have had to evolve a set of complex feeding tools because detaching, ingesting, and grinding epilithic algae is difficult (Arens 1989). In addition, alga grazers are confronted with the specific functional problem of mouthpart abrasion. Several morphological adaptations prevent the mouthparts of alga grazers becoming quickly ruined through use on rough stones (see later). Each of these different solutions to the same problem (so-called paradaptations, Bock 1959) has convergently been found by different grazers. Among the factors that have influenced a species to "decide" in favour of a particular evolutionary pathway, the organizational plan of its ancestors, i.e., its preadaptations, is certainly the most important. For example, replacement of deteriorated apparatus is the simplest solution to the problem of wear and tear for insect larvae because of their moulting habit. Vertebrates have other preadaptations. Furthermore, the extent of abrasion, and consequently the necessity for evolving effective protection against wear, depend strongly on the type of scraper used by the animal. A brush is more susceptible to abrasion than a sturdy gouge and shows different signs of wear.

These and other aspects should be considered in the following discussion of the different solutions to the problem of wear evolved by alga grazers. An exact quantitative analysis of the effectiveness of these solutions is impossible because the feeding rate, the pressure applied against the substratum, the details of mouthpart mechanics, and many other complex factors are unknown and, in most cases, may not be measurable. However, other data are often available, such as the way the mouthparts move (Schönmann 1981; McSchaffrey and McCafferty 1986, 1988; and others), the life-span, or the moulting rate, and this makes possible some estimation of the extent of wear and the value of the adaptations evolved.

Reduction of the speed of abrasion

On the assumption that the roughness of the substratum is constant, the speed of abrasion of a scraping apparatus depends on its resistance to wear, its frequency of use, and the degree of pressure with which it is applied to the stone.

Degree of pressure

Gouges, excavators, and rakes, which work solely by means of a thin cutting edge or a single row of structures, are especially susceptible to abrasion. On the other hand, in flat scraping tools like brushes and rasps, the pressure is spread over numerous fine structures so that the strain on each structure is not great. It is possible to illustrate this by means of a comparison. In scraping brushes (Figs. 2–4), the abrasion usually causes only the tips of bristles to be worn down. More extensive defects (Figs. 2*d* and 3*e*) are always restricted to a small part of the brush and are rarely found. Even in these exceptional cases, maximal deterioration of the structures amounts to 10–20 μm.

In contrast to this, gouges and excavators often completely lose their blades as a result of abrasion (Figs. 9*a*–9*d* and 11*a* and 11*b*). In adult animals, this represents the wearing down of a scraping apparatus by 100 μm or more, even when the duration of use is similar to that in animals possessing brushes.

Improvement of the wear resistance of the structures

To avoid damage, especially breakage, it is advantageous for the structures of the scraping apparatus to have a certain degree of flexibility. A good example of this is the slender scraping teeth of the armoured catfish *Ancistrus* (Fig. 23) (Arens 1989), which are composed of a gouge-like tip, a long shaft, and a bent root. Because of a flexible connection between shaft and root, the teeth can easily conform to the contour of the substratum, and the risk of their hard, but brittle, enamel tip being chipped is thus reduced. One could assume that it would also be advantageous for grazing arthropods to possess flexibly mounted rake prongs or scraping bristles. However, in these specimens, a trend towards rigid anchoring of such fine structures is observable. In convergent evolution, setae have lost their basal articulation and are fused with the integument, as can be seen in the case of the maxillular rake of *Ameletus* (Fig. 5) and the palpal brush of the Heptageniidae (Fig. 2) (Arens 1987). The reason for this is presumably the small size of arthropodan setae compared with algal cells. If the setae are too flexible, the arthropod is unable to detach algae firmly adhering to the substratum. Despite the rigid anchoring, the risk of breakage is low because of the mechanical properties of chitin.

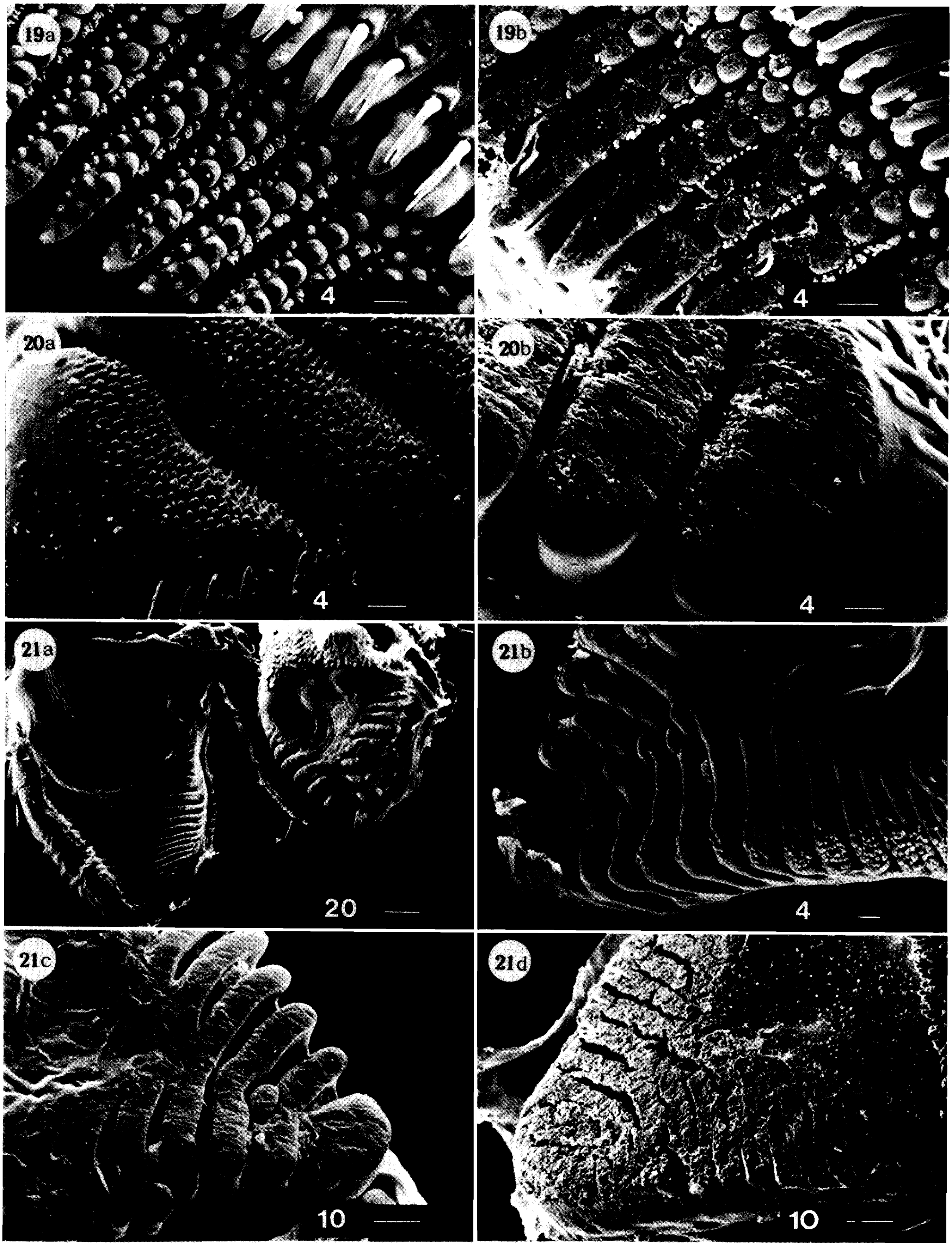
Another possibility for diminishing the speed of abrasion of scraping organs is the use of wear-resistant building materials. One example of this has already been described: the enamel coat on the teeth of the catfish *Ancistrus*. Most arthropods harden parts of their mouthparts by heavy sclerotization of the cuticle. All grazers in this study have adopted this strategy, but additional protection against wear and tear can be found in some species. *Ligia* and *Oxycera* deposit lime in their cuticle. Abrasion of their scraping tools is comparatively minor (Figs. 6, 8, 12, and 13), and other kinds of defects are a result of the brittleness of the calcified cuticle; in *Ligia* small fragments of the mandibular blade break off (Fig. 12*b*), and in *Oxycera* the brittle cuticular layer delaminates (Fig. 6*c*). Presumably, other minerals harder than lime will be detected in the cuticle of scraping organs. I intend to carry out investigations similar to those of Hillerton and Vincent (1982), who have detected zinc and manganese in parts of the mandibles of many insects from different taxa. The cutting edges of locusts, mandibles, for example, have been shown to be twice as hard as the rest of the mandible (Hillerton et al. 1982). Some marine snails have evolved similar adaptations: *Patella* deposits Fe_2O_3 and fluorapatite in the teeth of its radula, and the rasping structures of *Chiton* and *Littorina* contain magnetite or gypsum (Lowenstam 1962). Chemical analysis will show whether the teeth of the radula of *Ancylus* lack similar hardening agents. Their extensive abrasion (Fig. 15) seems to indicate this.

In addition to hardening by deposition of minerals, the cuticle or other integuments can be adapted to resist wear by modification of their microanatomy. Frequently, scrapers with a cutting edge are composed of layers of cuticle of different degrees of hardness. This construction guarantees the robustness of the apparatus, while allowing the scraper to sharpen itself during use (Figs. 9, 11, and 14). Well-known examples of analogous constructions are the teeth of rodents and Aristotle's lantern of sea urchins. That this specific microanatomy has also evolved in insects was not previously known. It is obviously not a common characteristic but represents an adaptation of some scraping organs to deal with the problem of wear. Evidence for this is (*i*) that this microanatomy is restricted in *Baetis* to the heavily sclerotized distal part of its gouge blade (Fig. 9), (*ii*) that it is not found in all scraping organs (e.g., Fig. 10), and (*iii*) that the weaker cuticular layers do not always have the same structure (cf. Figs. 9*e*, 14*d*, 14*e*). The latter observation strongly suggests the convergent evolution of this adaptation for scraping in insects from different taxa.

Frequency of use

The speed of abrasion of a scraping apparatus depends greatly on the duration of its use. The feeding activity of alga grazers

FIG. 19. *Rhithrogena*, showing fine structures of the molar surface. (*a*) Middle part of the right molar surface from a freshly moulted larva. (*b*) Worn fine structures from the exuviae of the same specimen. FIG. 20. *Lepeorus*. Fine structures of the molar surface. (*a*) Proximal part of the left molar surface, completely intact. (*b*) Same structures on a worn mandible. FIG. 21. *Oxycera*, grinding tooth above the pharyngial mortar. (*a*) Grinding tooth, general view. (*b*) Proximal part of the grinding tooth, unused. (*c*) The same structures of a moderately worn tooth. (*d*) Extremely abraded grinding tooth; note that only rudiments of the deep furrows between the masticatory ridges are still present.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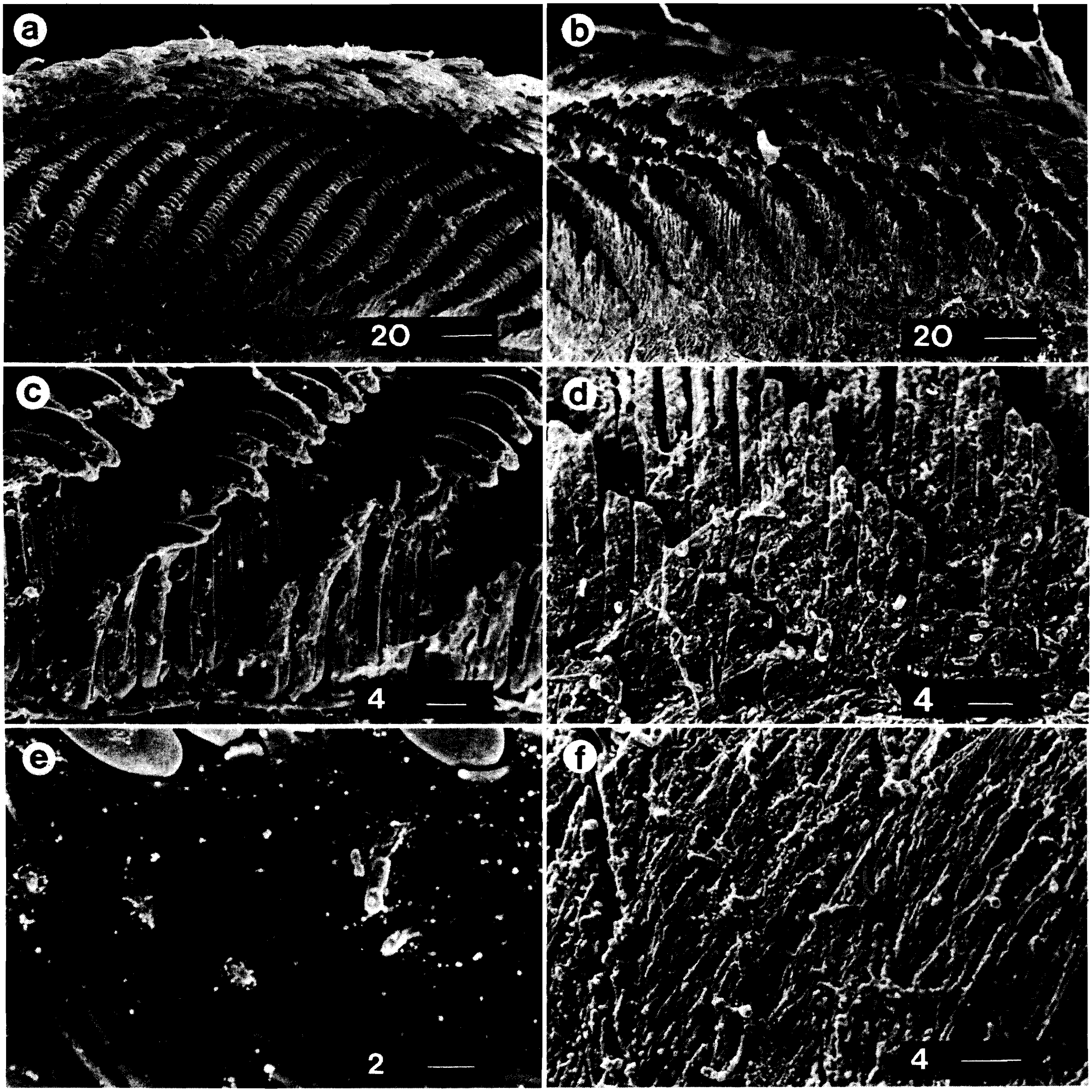

FIG. 22. *Epeorus*, showing correlation between the roughness of the substratum and the degree of wear of the palpal scraping brush (micrographs of the exuvia). (*a*) Labial palpal brush of a larva that has scraped for 11 days on smooth clay discs. (*b*) Same brush on the same larva, one moult later, after the larva has grazed for 12 days on sandpaper (grade 280). *c* and *e* show details from *a*; *d* and *f* show details from *b*.

in their natural habitat has never been investigated, but certainly differs to some extent from taxon to taxon. The important aspects of estimating feeding activity are the liveliness of an animal, its rate of growth, the efficiency of its mouthparts, and its exploitation of the food. Moreover, some species (e.g., mayflies and stoneflies) have to produce eggs or sperm during their larval phase because they are unable to ingest food after metamorphosis. In general, it would be expected that the food requirement of larvae (e.g., Ephemeroptera, Plecoptera, and Trichoptera) is greater than that of imagines (e.g., Elmidae). Presumably the feeding activity of lively mayfly larvae is especially high. In a laboratory stream (11°C, July) *Ecdyonurus* grazed for an average of 3 h daily (Schweder 1985).

Level of efficiency maintained relative to specific construction or use

Arthropods can replace worn scraping apparatus only when they moult. The tools used by each stage, therefore, have to last for a whole moulting interval. Subsequent abrasion of the tools may result in a gradual diminution, or even loss, of effectiveness.

Alga grazers that have evolved gouges can easily solve this problem by lengthening the gouge blades. If these blades become progressively worn down, their effectiveness is unimpaired as long as the cutting edge is sharp and the gouges can still reach the substratum. The trichopteran larva *Glossosoma* possesses this adaptation (Fig. 11). Its mandibular gouges are equipped with extraordinarily long blades (compared with those

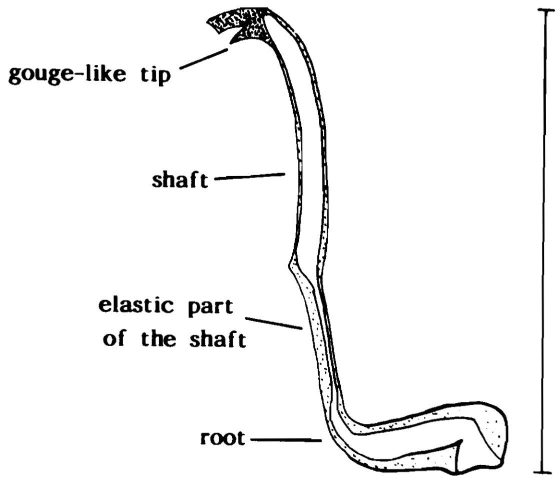

FIG. 23. Scraping tooth of the catfish *Ancistrus*.

of nongrazing species); even extremely worn gouges can reach the substratum because all the mouthparts around the mandibles are soft and compressible.

In other types of scraping apparatus, especially brushes, abrasion cannot be countered in this way. Bristles of brushes would lose their stability as a result of any elongation. Moreover, the tip of scraping bristles is always curved or equipped with prongs. As soon as this tip is rubbed off, the efficiency of such a sickle-shaped or a comb-shaped bristle is diminished considerably despite its extended shaft. In arthropods, the only possible way of maintaining the efficiency of the brushes is to use different areas of the brush in succession. Most of the species chosen for this study do this. For example, the ephemeropteran larva *Epeorus* presses its palpal brushes at an angle against the substratum, so that at first only bristles along the front of the brush lose their tips (Fig. 2*c*).

A third strategy for maintaining the scraping apparatus can be observed in *Oxycera*: the combination of coarse with fine tools (Figs. 6–8). A very coarse and therefore wear-resistant rake loosens the attached algal layers, but cannot effectively sweep up the detached food. This is the main task of the other two rakes which consist of more delicate structures. Because of its solid construction, the coarse rake retains its efficiency for a long time despite abrasion.

Replacement of abraded apparatus and structures

Even if the abrasion of scraping tools can be delayed and the consequent reduction in their effectiveness restricted for a time, abraded structures must be replaced sooner or later. There are two possibilities: (*i*) successive exchange of single worn structures for newly produced ones; (*ii*) moulting, in the course of which an abraded scraping apparatus is entirely shed and an intact replacement released.

Successive exchange of single structures

This method of repairing damaged scraping tools can be used by grazing snails and vertebrates; arthropods are incapable of replacing structures one by one because of their exoskeleton.

The scraping organ of snails, the radula, is a long chitinous band studded with hard teeth. Only its distal part makes contact with the substratum. As the radula dissolves distally (as a result of abrasion and enzymatic decomposition), it increases basally, so that unused radula sections are continuously put into action. The edible snail *Helix* produces four rows of teeth daily (at 23°C, Menzel 1976). Especially high rates of growth have been measured in the radula of snails that graze on rocky shores (Graham 1964). However, in *Ancylus* the pharyngeal blind sac, wherein the radula is formed, is not noticeably lengthened, therefore one can assume that the growth of the radula is not unusually rapid.

The catfish *Ancistrus* has a polyphyodont dentition. Its replacement teeth develop in numerous epidermal lamellae which fill a trench on its excavated jaws. If a tooth is fully developed, it pushes through the epidermis and becomes erect. After the tooth has reached its working position, its root and the jawbone grow together (Rauther 1911). Thus, *Ancistrus* does not replace teeth in rows, as do sharks and some other fish, but one by one (cf. *Garra*).

A convergent mechanism has been evolved by anuran larvae. Tadpoles scrape on algal pastures by means of small horny denticles which are arranged in rows on the lips. Underneath each of these visible structures several replacement denticles are positioned in such a manner that the tip of each projects into the hollow interior of the one above. New structures are continuously being added to this series from below (Gutzeit 1890). Because the denticle on the outside falls out from time to time, the replacement denticles are put into action one after another.

Moulting: exchange of the whole scraping apparatus

Arthropods: Growth, development, and regeneration in arthropods involve the moulting of the exoskeleton. Crustaceans, myriapods, and apterygotous insects are capable of moulting throughout their life, whereas in winged insects, ecdyses are confined to the larval stages. The number of moults differs considerably from taxon to taxon. There is no clear explanation for this. For example, there is no correlation between the number of instars of a species and its final size. There are even cases in which an ecdysis does not result in an increase in size or a more advanced state of development (Schuhmacher 1970; Beck 1972).

Another function of ecdysis has rarely been considered: moulting for the purpose of replacing worn cuticular structures. Frequent ecdyses should be advantageous for grazing arthropods because of the severe abrasion of their mouthparts. Indeed, an increased number of instars can be demonstrated in two insect families that contain mostly alga grazers: (*i*) The Heptageniidae (*Epeorus*, *Rhithrogena*, and other highly specialized grazers) have approximately 50 instars (Ide 1935; Gros 1923). In comparison, mayfly larvae of other families (e.g., *Baetis*, *Baetisca*) moult 10–30 times (Brittain 1976; Illies 1968; Illies and Masteller 1977; Pescador 1973; Pescador and Peters 1974; Trost and Berner 1963), the larvae of stoneflies (P. Zwick, personal communication) and dragonflies (O'Farell 1970) only 10–15 times. Because it is still impossible to breed heptageniid mayflies in the laboratory from egg to subimago, their number of instars must remain an estimate, but doubtless it is higher than in all other pterygotous insects. I found moulting intervals of ca. 10–12 days at 12°C in almost fully grown *Epeorus* larvae (Table 1). If more frequent ecdyses occur in younger larvae and there is a univoltine cycle, a mean moulting interval of only 1 week would seem to be normal in the Heptageniidae. I have obtained similar values (8–12 days) for *Brachyptera* (Plecoptera), which certainly has fewer instars but develops within a few months. (*ii*) Larvae of holometabolous insects rarely moult more than 10 times during their larval phase. For example, caddisflies usually have five instars (Kanter 1966; Nielsen 1942; Schröder 1976). There is only one known exception: in the Glossosomatidae, which are highly specialized alga grazers, the number of larval stages reaches seven (Kanter 1966) or even eight (Castro 1975). This is obviously an apomorphic character because the Rhyacophilidae, the sister-group of the Glossosomatidae, have five instars (Nielsen 1942), as do other caddisflies.

However, it should be noted that the maximal degree of wear is comparable in most grazing insects, although some species moult over intervals of only 1–2 weeks (e.g., Figs. 2 and 3), whereas the moulting intervals of others last up to a few months, as in *Liponeura* (four instars, Fig. 14). *Limnius* and other riffle beetles can scrape the whole year long using the same set of mouthparts (Fig. 4).

In addition to a general shortening of the moulting intervals, it would be a great advantage if the frequency of ecdyses of an animal could vary in accordance with the amount of wear to which the mouthparts are subject. One might expect to find such a flexible response in mayflies and other more primitive insect orders particularly, because the number of their instars is not fixed but depends to a certain degree on external factors (food, temperature, damage, etc.) (Hübner 1902; Oppenheim 1908; Goss 1974). Theoretically, there are two ways in which an animal could detect defects in its mouthparts. On the one hand, an animal may perceive damage indirectly because it would take longer to fill its gut, despite an unchanged algal pasture. But damage could also be perceived directly. The prerequisite for the latter is innervation of the scraping structures. As far as was discernible from 2-μm sections, this condition is met by the sickle-shaped bristles of the *Epeorus* brush. The induction of ecdysis caused by the loss of innervated bristles is known in some arthropods. *Thermobia* (Zygentoma) moults after a certain number of its scales (innervated sensillae) have been stripped off (Sahrhage 1953; Larink 1976). In *Daphnia*, amputation of the bristles of its antennae induces early ecdysis (Hübner 1902).

An analogous reaction could not be found in *Epeorus* (Table 1). Heptageniid larvae do not seem to have employed this strategy to prevent wear.

Pisces: The cyprinids *G. taeniata* and *L. bicolor* and the homalopterid *Gastromyzon punctatulus* are highly specialized grazers. These fish occasionally shed the horny rasp coat on their jaws. Moulting of external horny structures was previously unknown in fish, with the exception of the rasp organ of lampreys (Giersberg and Rietschel 1967).

The evolutionary importance of wear of the grinding apparatus

Because of their function, all types of grinding apparatus must have a solid and hard construction, so that their susceptibility to wear and tear is low. Nevertheless, extensive damage arises if the food of an animal is harder than the building material of its grinding organs. For example, the molar surfaces of grasshoppers (Chapman 1964) and the teeth of horses are rubbed off considerably by chewing grass that contains silicates.

The food of alga grazers is also a problem in this regard because of its high content of diatoms and crystalline sediment. Most grazing insects grind their food by means of mandibular molar surfaces; gizzards are obviously unsuitable for crushing epilithic algae (Arens 1989). However, *Oxycera* has evolved a pharyngial mortar. The construction of a mandibular press is impossible for this dipteran larva because its mandibular–maxillary complexes do not work against one another but side by side. In this species, wear of its masticators can render them almost useless (Fig. 21).

In all other grazers in this study, masticators wear down more slowly than scraping tools; when the latter have deteriorated considerably, molar surfaces are only smoothed. Certainly this diminishes the friction force of a grinding apparatus, but its usefulness for chewing is not endangered, providing that gratings, ridges, and other coarse structures exist. Scrapers are therefore much more problematic with regard to abrasion. In this situation, only low selection pressures may be necessary to encourage additional improvements in the wear resistance of masticators of alga grazers.

Conclusions

Some of the mechanisms discussed above for solving the problem of wear have evolved only during adaptation to grazing on algae; others were already present as preadaptations in the respective ancestors. In my opinion, one indication of the great importance of favourable preadaptations is the fact that worldwide, insect larvae are the most important grazers in streams, whereas only few insect imagines harvest epilithic algal layers. One reason for this is probably the inability of adult insects to repair their mouthparts by moulting. In this connection, it should be noted that hemimetabolous insect orders (Ephemeroptera, Plecoptera) in all parts of the world have been especially successful in evolving alga-grazing species. For example, mayfly larvae of different families and genera live as specialized grazers in streams on all continents and have adapted themselves by convergent evolution to this food source (e.g., the Heptageniidae in the northern hemisphere, and the Leptophlebiidae in the southern hemisphere). The same is true of stonefly larvae. A relatively large number of instars (ca. 15) and short moulting intervals are typical of both orders, even in species feeding on detritus which is probably the primary food of mayfly and stonefly larvae. It is possible that this favourable preadaptation to deal with the problem of wear is an important reason for the multiple evolution of alga grazers.

However, it is obvious that one advantageous preadaptation alone is insufficient to solve the problem of wear. For example, brushes are very effective scraping tools (Arens 1989), but they are especially susceptible to abrasion, since they are constructed of delicate bristles. The palpal scrubbing brushes of the Heptageniidae wear down so quickly that the larvae must have several adaptations: short moulting intervals, stepwise wearing down of the brushes, and evolution of two pairs of brushes (*Rhithrogena* and *Epeorus*). Other types of scraping apparatus (gouge, excavator) do not pose as many problems with regard to wear, but are probably less effective in detaching epilithic algae. For many insects, however, the evolution of these types of apparatus was the best solution, given the preadaptations. Either their ground plan did not permit the construction of the most effective tool (Arens 1989), or it was impossible for them to cope with the swift deterioration of, for instance, a brush. The scraping apparatus most prone to wear is doubtless the rake because it works on the substratum with only one row of usually delicate structures. Even in this case, however, a solution to the problem has been found: the work is divided between several rakes having different degrees of coarseness, as in *Oxycera*.

In my opinion, SEM investigation of defects arising from wear will in future provide us with a much better understanding of the function and adaptation of feeding organs, especially of insect mouthparts. The feeding mode of aquatic grazing species can be recognized by means of their abraded scrapers, since the feeding organs of detritivores, filter feeders, and predators in streams show, at most, insignificant wear. On the basis of indications of abrasion, one can clearly and easily demonstrate which mouthparts make contact with hard materials and which do not. For example, the direction in which scratches run on worn molar surfaces (Fig. 20*b*) indicates that the mandibles of mayfly larvae are capable of grinding movements, in spite of three articulations. This is a long-debated question (Strenger 1953; Brown 1961; Schönmann 1981). Similar progress in the settling of functional or morphological questions can be expected for many other groups of animals, e.g., digging and boring insects.

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