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RETENTION OF TRACHEAL GILLS IN ADULT EPHEMEROPTERA AND OTHER INSECTS

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Abstract: The European species of Ephemeroptera (and a representative sample of extra-limital species) were examined in search for possibly occurring remnants of larval gills. They occur regularly in subimagoes and imagoes of *Palingenia longicauda* and *P. fuliginosa* (Palingeniidae), irregularly in subimagoes of *Ephoron virgo* (Polymitarcidae); they are missing in other genera though some structures of their bases may be retained. Accessory gills are retained on maxillae and bases of fore legs in subimagoes and imagoes of *Isonychia ignota* (Isonychiidae). These cases are described and illustrated; there is always a progressive reduction of gills from the larva to the imago. Furthermore, retention of accessory gills in the genera *Murphyella*, *Coloburiscus* and *Coloburiscoides* (Siphonuridae, Coloburiscinae) and abdominal gills in *Plethogenesia* (Palingeniidae) and *Ephemerella* subg. *Timpanoga* (Ephemerellidae) is described and illustrated; it is similar to that of the European genera. The cases of retention of larval tracheal gills by adults of other insect orders (Odonata, Plecoptera and Trichoptera) are briefly reviewed, and the functional, developmental and evolutionary significance of these phenomena is discussed.

Among the five truly amphibious insect orders with almost universally aquatic juvenile stages and terrestrial adults*), retention of tracheal gills in adults is common and generally known in the Plecoptera, widespread though rarely mentioned in the Trichoptera, and probably also occurs in a few calopterous Odonata. There are only internal remnants of gills in the adults of anisopterous Odonata and Megaloptera, and the cases of retention of abdominal or accessory gills in the Ephemeroptera have remained unknown or were only passingly mentioned in ephemeropterological literature and have escaped the attention of general entomologists. We report for the first time on the occurrence of abdominal gills in adults of *Palingenia*, *Plethogenesia* and *Ephoron* species and of accessory gills in species of Coloburiscinae (Siphonuridae), and provide first details on the retention of the former in *Ephemerella hecuba*

*) Larvae of some Odonata and many Plecoptera are terrestrial, one species of Plecoptera is aquatic in the adult stage, and larvae and pupae of several species of Trichoptera are terrestrial (ripicolous).

and of the latter in *Isonychia* species. The reported cases of retention of tracheal gills or their remnants by adult insects are reviewed and the significance of this phenomenon is discussed. The initial discovery of the occurrence of gills in the adult stages of *Palingenia* has been made by the senior author who also contributed to discussion; a detailed examination of mayflies has been carried out by the junior author.

Tracheal gills in larvae of Ephemeroptera - review and literary data on metamorphosis

Tracheal gills of the larvae of Ephemeroptera are of two kinds:

a) Segmental paired abdominal gills are universally present with the exception of the genus *Murphyella* LESTAGE (Siphonuridae), usually laterally or dorsally, rarely ventrally (Behningiidae, 1st pair in the Oligoneuriidae), primitively on segments I—VII (I—IX in some fossil forms), apomorphically on II—VII, III—VII, IV—VII, I—VI and I—V. Originally a gill probably consisted of a single plate or of a plate and a tuft of filaments (cf. RIEK, 1973); this condition has been retained (e. g. Isonychiidae, Oligoneuriidae, Heptageniidae), or only the filaments (e. g. Ephemerioidea incl. Behningiidae, Palingeniidae, and Polymitarcidae), sometimes secondarily fused together and forming a plate (some Leptophlebiidae), or mostly only the plate, sometimes doubled (e. g. some Baetidae, Siphonuridae), have remained. Sometimes the gills, especially the first two pairs, are strongly reduced, or modified into opercula, adhesive discs, etc. The gills are mostly missing in the first larval instar.

b) Accessory gills are always filamentose and are situated on the anterior parts of the body in four families, as follows: (i) Siphonuridae: Coloburiscinae (in all their genera; always on maxillae, sometimes on labium, fore coxae and thoracic sterna), (ii) Isonychiidae (on maxillae and near to the bases of fore coxae), (iii) Baetidae (in some genera only: on maxillae in *Afrobaetodes* DEMOULIN, near to the bases of fore coxae in *Heterocloeon* McDUNNOUGH and some species of the genera *Baetodes* NEEDHAM & MURPHY and *Dactylobaetis* TRAVER & EDMUNDS), (iv) Oligoneuriidae (on maxillae).

The gill base remains unmodified in families with fine, unmodified gills (e. g. Baetidae, Siphonuridae, Heptageniidae), only the hind margin of the tergum is moderately arcuately emarginate at place of gill insertion. In the families with robust gill plates (e. g. Ephemeridae, Palingeniidae, Polymitarcidae) the tergal cuticle is markedly thin and depressed at each gill base; moreover, a narrow semi-ring-shaped sclerite, strengthening the gill base medially, may be developed.

Literature on the metamorphosis of tracheal gills is scanty. PALMÉN (1877) stated that in some species the tracheae of all or at least some of the abdominal spiracles do not moult during the larval-subimaginal ecdysis. LANDA (1948, 1949) studied 30 species of 21 Central European genera and did not find any remnants of gills in subimagos and adults (*Palingenia* and *Isonychia* were not studied). He found that during the larval-subimaginal ecdysis the abdominal gills do not moult and remain full and intact on the exuviae. Also their tracheae do not moult, remaining

within the gills and being shed together with them. However, the proximal simple part of trachea branchialis moults normally as the other tracheae of the body. The opening remaining after the lost gill in the cuticle of the subimago is closed, but the spiracle (which in the larva served only for the pulling out of the old tracheal intima) remains open; the trachea arcus lateralis (directly connected with the lateral tracheal trunk) does not close either. NEEDHAM, TRAVER & HSU (1935) and LANDA (1969) noted that the tufts of the filaments of accessory gills are retained by the adults of the genus *Isonychia* EATON.

ALLEN & EDMUNDS (1959) and EDMUNDS, JENSEN & BERNER (1976) briefly mentioned retention of abdominal tracheal gills by subimagos and imagoes of the Nearctic species *Ephemerella* (*Timpanoga*) *hecuba* (EATON); it occurs in both its subspecies and has been regarded as a diagnostic character differentiating the monotypic subgenus *Timpanoga* NEEDHAM from the other subgenera of *Ephemerella* WALSH.

BIRKET-SMITH (1971) found in adult *Povilla adusta* NAVAS (Polymitarcidae) from Ethiopia that longitudinal folds forming the dorsal edges of the membranous »pleural area« of abdominal segments 2—7 are each marked in their caudal thirds by a small, vortex-like structure, and that both »intrinsic pleural muscles« are attached to these vortices. Since these muscles are identical with stronger and more elaborate gill muscles of the larva, Birket-Smith correctly concluded that »the vortex in the imago is the remain of the now obliterated gill appendage«. Referring only to this finding KUKALOVA-PECK (1978) remarked that »articulated abdominal wings ... aer sometimes noticeable as vestiges in mayfly adults.«

MATERIAL

With the exception of the genus *Prosopistoma* LATREILLE (Prosopistomatidae) representative species of all European genera of Ephemeroptera (alcohol-preserved imago, in many cases also subimago; coll. Institute of Entomology, Praha) and of more than 30 extralimital genera from all zoogeographical regions and all recognized families were examined. *Palingenia fuliginosa* (GEORGI) and *P. longicauda* (OLIVIER) (E. Slovakia, Latorica R., Leles, 65 larvae, 12 subimagos, 8 adults) served as model species for the study of the genus *Palingenia* BURMEISTER (Palingeniidae), *E. virgo* (OLIVIER) (S. Bohemia, Lužnice R., Bechyně, 6 larvae, 250 subimagos, 68 adults) for *Ephoro*, WILLIAMSON (Polymitarcidae), and *I. ignota* (WALKER) (Bulgaria, Golyama R., Biser, 13 larvae, 3 subimagos, 6 adults) for *Isonychia* EATON (Isonychiidae).

Material of extralimital species examined in detail:

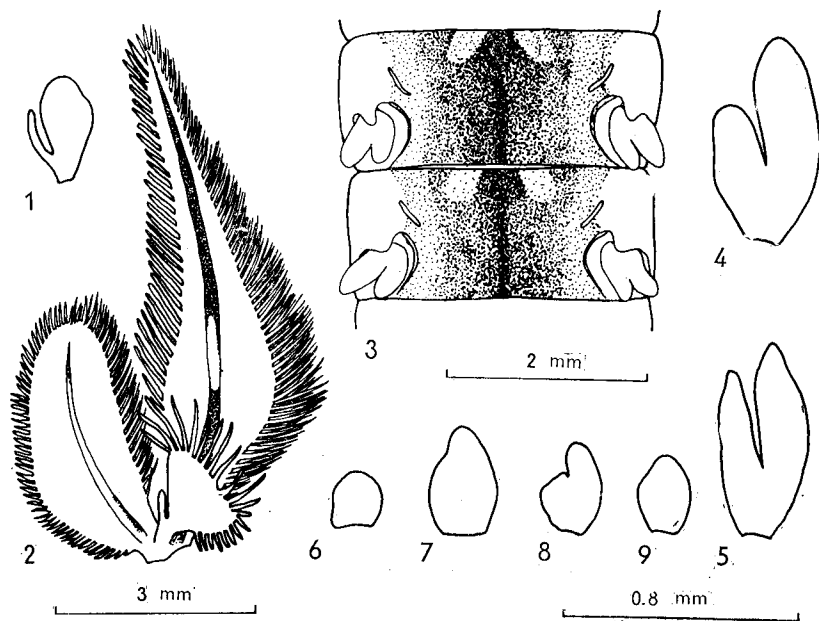
Palingeniidae: *Plethogenesia lieftincki* DEMOULIN (Papua-New Guinea, Sapik R., above Ambunti, 17. v. 29, coll. G. F. Edmunds, Salt Lake City, 2 ♂♂), *Plethogenesia* sp. (Papua-New Guinea, Pupari R., 200 km from mouth, xi. 74, leg. Fisheries Dept., Port Moresby, coll. W. L. Peters, Tallahassee, 1 ♂, 1 ♀); Ephemerellidae: *Ephemerella* (*Timpanoga*) *hecuba* (EATON) (Idaho, Bonner Co., Priest R., 5 mi N of Priest, 10. viii. 64 leg. and coll. G. F. Edmunds, 7 larvae; Montana, Ravalli Co., Bitter Root R., 10 mi S Darby, 25. viii. 64 leg. and coll. G. F. Edmunds, 1 subim., 2 ♂♂, 1 ♀); Siphonuridae: *Murphyella needhami* LESTAGE (Chile, W of Angol Crest of Sierra Nahnelbuta, 1 & 3. i. 51 leg. Ross & Hickbeibacker, coll. G. F. Edmunds, 2 larvae, 1 subim.), *Murphyella* sp., (Chile, Nuble Prov., Rio Niblinto, 35 km E of Coihnero, 19. i. 68, leg. L. Peña, coll. G. F. Edmunds, 1 ♂, 1 ♀), *Coloburiscoides* sp. (Australia, N. S. W., Mongalowe R. at Monga, 6. ii. 66, leg. and coll. G. F. Edmunds, 3 ♀♀, 15 larvae), *Coloburiscoides* sp. (Australia, N. S. W., Gang Gang Creek, Kiandra, 13. xii. 74 leg. E. F. Riek, coll. Soldán, 12 larvae), *Coloburiscus humeralis* (WALKER) (New Zealand, Carterbury Prov., Hawdon R., at junction with Sudden stream/trib. Waimakiriri R., 6 mi N of Cass 3. iii. 66, leg. and coll. G. F. Edmunds, 5 larvae, 5 subim., 4 ♀♀).

RESULTS

Most of the European genera do not possess tracheal gills in the adult stages. Their remnants commonly occur only in *Palingenia* and occasionally also in *Ephoron*. In some genera (*Ephemera* L., *Behningia* LESTAGE) there are (both in subimaginal and imaginal stages) retained cuticular structures pertaining to the bases of larval abdominal gills. Although the bases of larval gills are strongly modified in the adult stages and the opening of the trachea arcus lateralis is closed, the semi-ring-shaped sclerite encircling the original opening of trachea arcus lateralis is distinct.

Remnants of the accessory gills are retained only in *Isonychia*; the accessory gills of Oligoneuriidae (the European genera *Oligoneuriella* ULMER and *Oligoneurisca* LESTAGE, and an American genus *Lachlania* HAGEN have been examined) are not brought along to the adult stage.

As far as the extra-European genera are concerned, the remnants of accessory gills were found in imagoes and subimagoes of all three described genera of the Neotropical, Australian and New Zealand subfamily Coloburiscinae (Siphonuridae), i. e. *Murphyella* LESTAGE, *Coloburiscoides* LESTAGE and *Coloburiscus* EATON, and the remnants of abdominal gills in the Papuan genus *Plethogenesia* ULMER (Palingeniidae) and in the Nearctic species *Ephemerella* (*Timpanoga*) *hecuba* (EATON) (Ephemerelli-



Figs. 1—9: Retention of tracheal abdominal gills in *Palingenia longicauda*. Fig. 1 — larva, gill 1. Fig. 2 — larva, gill 3. Fig. 3 — subimago, abdominal terga III and IV, dorsal view. Figs. 4, 5 — subimago, abdominal gills 3 and 7. Figs. 6—9 — adult, remnants of abdominal gills.1

dae); these cases are more fully reported below. Remnants of cuticular structures of gill bases were found in adults of extra-European species of the following genera: *Ephemerella* WALSH (Ephemerellidae); *Tricorythus* EATON, *Leptohyphes* EATON, *Tricorythodes* ULMER (Tricorythidae); *Euthyplocia* EATON, *Campylocia* NEEDHAM & MURPHY, *Probosciodoplocia* DEMOULIN (Euthyplociidae); *Ichthybotus* EATON, *Eatoni-genia* ULMER (Ephemeridae); *Campsurus* EATON, *Tortopus* NEEDHAM & MURPHY, *Asthenopus* EATON, *Povilla* NAVÁS (Polymitarcidae); *Caenis* STEPHENS, *Brachycercus* CURTIS, *Tasmanocoenis* LESTAGE (Caenidae). Remnants of accessory and abdominal tracheal gills were found also in several Nearctic species of the genera *Isonychia* and *Ephoron* respectively; their structure and course of their developmental reduction are the same as in the European species described below.

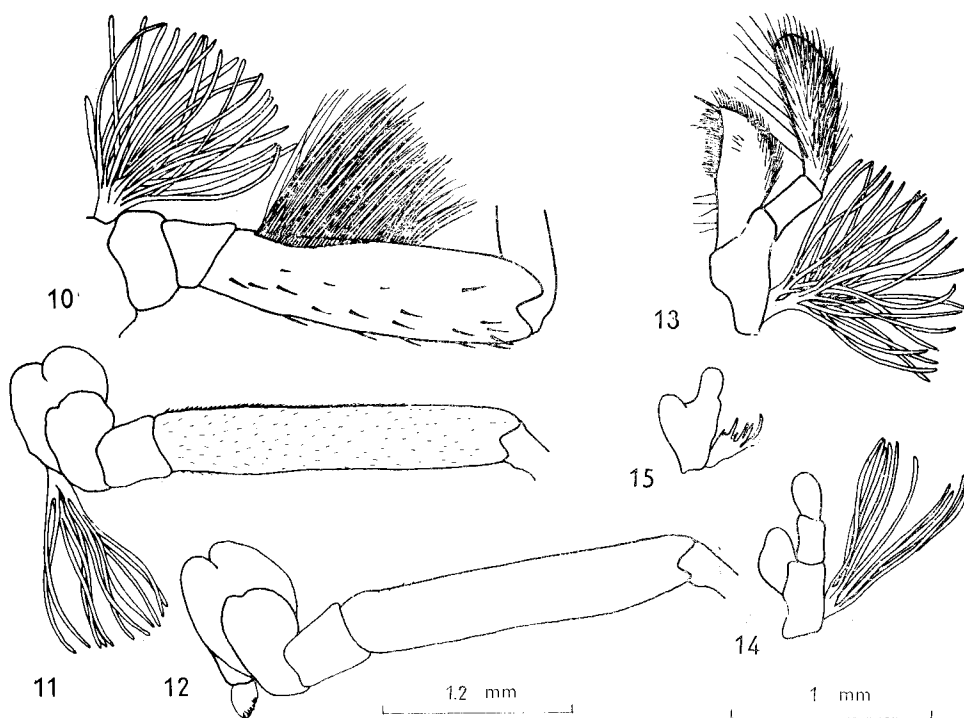
a) *Palingenia fuliginosa* (GEORGI) and *P. longicauda* (OLIVIER) (Palingeniidae) - abdominal gills. Larva. Gills 2—6 (Fig. 2) large, biramous, with a fringe of numerous filaments. Anterior part elongate and pointed, posterior part shorter and rounded. Gill 7 biramous, both parts of equal size. Gill 1 (Fig. 1) strongly reduced, biramous, without filaments and visible trachea branchialis. Base of gill 1 also reduced without sclerite encircling the opening of trachea arcus lateralis. Subimago (Figs 3—5). Gill 1 missing, its base no more discernible. Gills 2—7 white, non-sclerotized, without rounded apices of both lobes, the anterior lobes usually 1.3 times as long as the posterior one. Both lobes of gill 7 (Fig. 5) equally long. Not only the basic shape, but also the construction of gill bases (depression in tergum and semi-ring-shaped sclerite) as in larvae; however, trachea branchialis is missing, although the association of each of the gills with trachea arcus lateralis is retained. The adult spiracle opens as an elongate oblique split in front of each gill base (Fig. 3). Imago (Figs 6—9). The size of the remnant of gill plates decreased by 1/3 to 1/2, conspicuous differences in size occurring even in the same individual. Some gill remnants with indication of the original two lobes (Figs 7, 8), others simple, small, scale-like (Figs 6, 9). Bases of gills 2—7 almost unmodified in comparison with the subimago.

b) *Plethogenesia lieftincki* DEMOULIN and *Plethogenesia* sp. (Palingeniidae) - abdominal gills. Larva (not examined) fide ULMER (1939). Gills of the same type as in *Palingenia*; first pair reduced, the others biramous with unequally long and shaped branches. Imago. Gill remnants very similar to those of *Palingenia* but somewhat smaller. First pair absent, remnants of the others (not necessarily complete) often - as in *Palingenia* - of unequal shape and size.

c) *Ephoron virgo* (OLIVIER) (Polymitarcidae) - abdominal gills. Larva. Gills 2—7 biramous with marginal filaments; both anterior and posterior branches pointed and approximately equally long. Gill 1 reduced similarly as in *Palingenia*. Subimago. Some specimens (28 out of 250 examined) with gill remnants on various segments; gill 1 always missing. Gills scale-like, mostly rounded, approximately 0.2—0.3 mm long, occurring mostly on terga II—IV. Gill bases (depression and semi-ring-shaped sclerite) well developed on terga II—VII. Imago. No gill remnants were found.

d) *Ephemerella* (*Timpanoga*) *hecuba* (EATON) (Ephemerellidae) - abdominal gills.

Larva (Figs. 17, 27). Gills present on segments IV—VII, the others completely reduced. Gill 4 the largest, semi-operculate, oval, postero-medially arcuately elongate, covering the others (Fig. 17). Gills 4 and 6 somewhat smaller but similarly shaped; gill 7 strongly reduced (as long as $1/5$ — $1/4$ of gill 4), anteriorly bilobate, laterally deeply emarginate, with well visible tracheae (Fig. 27). All gills composed of a dorsal plate and two fine ventral lamelliform lobes composed of a number of circular lamellae. Gill plates 4—6 brownish with some dorsal spines and setae, plate 7 and all lamellae colourless. Subimago (Figs. 16, 28). Gill remnants quite differently shaped: narrow, lobiform, rounded to obtusely pointed (gills 4, 5) or distinctly pointed (gills 6, 7), simple*), gills 6, 7 about 2—3 times as long as gills 4, 5 (a contrary condition to that of the larva!). Gills (particularly their mid-lines) with ferruginous to dark brown pigmentation. No subimaginal and imaginal gill linked into the tracheal system. Imago (Fig. 29). Gills of the same shape as in the subimago but about half as long present on segments IV—VII; gill 7 again 2—3 times as long as gill 4.



Figs. 10—15: Retention of tracheal accessory gills in *Isonychia ignota*. Figs. 10, 13 — larva. Figs. 11, 14 — subimago. Figs. 12, 15 — adult. Figs. 10, 11, 12 — accessory tracheal gills of fore coxae. Figs. 13, 14, 15 — accessory tracheal gills of maxillae.

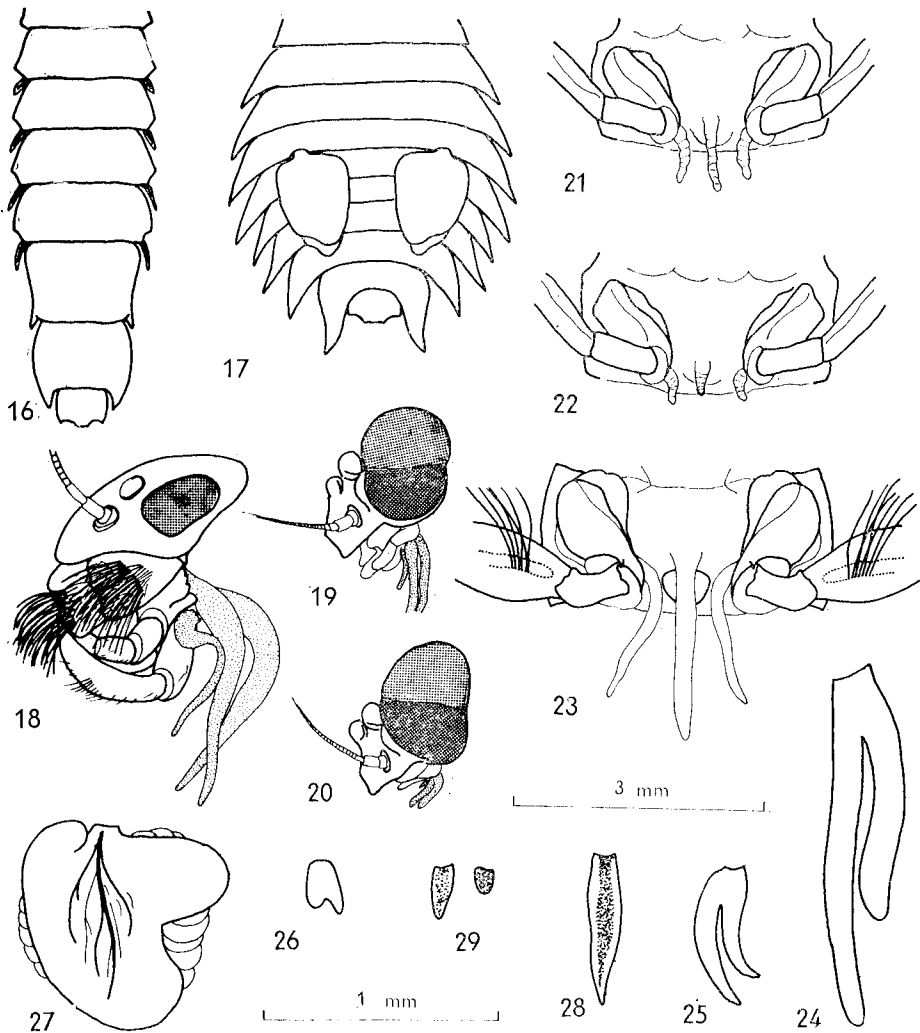
*) It is impossible to decide whether the subimaginal structures are remnants of plates or lamellae, but because of their simple shape the former alternative is more probable.

e) *Isonychia ignota* (WALKER) (Isonychiidae) - accessory gills. MAXILLA. Larva (Fig. 13): a rich tuft (20—30 filaments branching from a single stem) situated near the base of the maxilla. Subimago (Fig. 14): maxilla atrophied, but both fused galea & lacinia and 2-segmented palp (membraneous, desclerotized, all setae missing) discernible; tuft of filaments unmodified as far as size and shape are concerned, only the number of filaments reduced to 10—20. Imago (Fig. 15): atrophy of maxilla more advanced, its components hardly discernible; gills strongly reduced, only a few short filaments indicated. BASE OF FORE LEG (Figs. 10, 11, 12). The shape of accessory gill and progress of reduction from larva to adult similar as on maxilla; imago without remnants of filaments. Abdominal gills not retained.

Tracheal supply of accessory gills in *I. ignota* is of the usual type in the larva, with branchial gills directly joining the main tracheal trunks in the thorax (accessory gills of fore legs) and head (those of maxillae). In the subimago the trachea of accessory gills is closed similarly as the abdominal trachea arcus lateralis of other species.

f) *Murphyella needhami* LESTAGE and *Murphyella* sp. (Siphonuridae) - accessory gills. Larva (Figs 18, 23). Abdominal gills entirely absent; terga I—VII posterolaterally with thinner cuticle at places bearing the gills in related genera. Accessory gills finger-shaped, distally moderately narrowed, apically obtusely pointed, simple or branched (maxillary gills), paired or simple (sternal gills). Paired gills situated near to the bases of maxillae (branching subbasally, but leaving the maxilla distinctly as a single stem), labial palps (by about a half shorter, simple, distally markedly narrowed and sometimes almost S-shaped) and fore coxae (simple, mesally situated). Unpaired gills situated in the middle of pro-, meso- and metasternum (narrowly cylindrical, simple, the prothoracic ones about 1.3 times as long as the others). Thoracic gills connected by their tracheae with both the lateral tracheal trunks and cephalic gills with the cephalic tracheae (connection of maxillary gills similar to that of the genus *Isonychia* - cf. LANDA, 1969). Subimago (Figs 19, 21). All accessory gills distinct, the maxillary ones of two branches (length $2/3 - 1/2$ of larval gills), the labial ones simple, narrowly cylindrical, distally not narrowing. All thoracic gills finger-shaped, with wrinkled surface, as long as $1/2 - 1/3$ of larval gills. No subimaginal and imaginal gill linked into the tracheal system; the connecting tracheae closed, but their remnants distinct. Imago (Figs 20, 22). Gill remnants as in the subimago, both cephalic and thoracic gills shorter by about a half, maxillary gills with retained bifurcation, labial gills may be completely reduced.

g) *Coloburiscus humeralis* (WALKER) (Siphonuridae) - accessory gills. Larva (Fig. 24). Accessory gills situated only near the bases of maxillae; paired, flat, about as long as the maxilla, composed of two unequally long and apically rounded branches. Arrangement of tracheae the same as in *Isonychia*, *Murphyella* and *Coloburiscoides*. Subimago (Fig. 25). Accessory gills reduced to a third of their original length, their branches almost equally long, apically pointed. Tracheae connecting the accessory gills with the lateral tracheal trunks closed. Imago (Fig. 26). Gill



Figs. 16–29: Retention of tracheal accessory or abdominal gills in Coloburiscinae and *Ephemerella*. Figs. 16, 17, 27–29 — *Ephemerella* (*Timpanoga*) *hecuba*. Figs. 18–23 — *Murphyella* sp. Figs. 24–26 — *Coloburiscus humeralis*. Fig. 16 — subimago, terga IV–X. Fig. 17 — larva, terga II–X. Figs. 18, 19, 20 — head (lateral view) of larva, subimago and imago respectively; accessory gills dotted. Figs. 21, 22, 23 — prothorax (ventral view) of subimago, imago and larva respectively. Figs. 24, 25, 26 — maxillary accessory gills of larva, subimago and imago respectively. Fig. 27 — larva, gill 7. Fig. 28 — subimago - gill 7. Fig. 29 — imago, gills 6 and 4.

remnants short ($1/3-1/4$ of their subimaginal length), rounded, their bifurcation only slightly indicated. Abdominal gills not retained.

h) *Coloburiscoides* sp. (Siphonuridae) - accessory gills. Larva. Accessory gills only on head; simple, not branched, finger-shaped; 1 maxillary pair and 1 labial pair; labial gills slightly shorter and narrower, apically obtusely pointed. Subimago. Gills reduced to half the original length, of the same shape as in the larva; labial gills minute, hardly discernible. Imago. Labial gills completely reduced, maxillary gills situated on vestiges of maxillae minute and hardly discernible. Developmental changes of the system of gill tracheae the same as in *Murphyella*, *Coloburiscus* and *Isonychia*. Abdominal gills not retained.

Taxonomic distribution of perennibranchiality among Ephemeroptera

Retention of tracheal gills by adults has been observed in a rather heterogeneous assemblage of mayflies belonging to several evolutionary lines.

a) Accessory gills occur only in several groups of the suborder Schistonota*) and they have been retained by adult Isonychiidae and Siphonuridae: Coloburiscinae (both of Heptagenioidea); however, their abdominal gills have not been retained. Although opinions on the classification of these two groups vary*), they undoubtedly belong to the most ancestral evolutionary line of the order. Accessory gills of the more apomorphic Schistonota (Baetidae, Oligoneuriidae: Chromarcyinae, Oligoneuriinae) are not retained by the adults. The taxonomic distribution of both larval accessory gills and their atracheate adult remnants (there is no palaeontological evidence) seems to suggest that their presence is a plesiomorphic character; on the other hand, common sense and situation in other insect orders suggest that they have evolved as secondary structures supporting the function of abdominal gills.

b) Abdominal gills have been retained in an atracheate condition by adults in two families (Palingeniidae, Polymitarcidae) of the specialized superfamily Ephemerioidea of the suborder Schistonota and in a single subgenus of the family Ephemerellidae which is the most ancestral group of the more apomorphic suborder Pannota. The presence of abdominal gills in larvae is definitely plesiomorphic; this is also supported by paleontological evidence (cf. KUKALOVA-PECK, 1978). In spite of the present, rather mosaic-like, distribution of adult abdominal gills in modern mayflies, we may assume that this phenomenon had probably been widespread in their ancestors and that these remnants were probably better developed and tracheate. The argument is developed below, but one of the pertinent pieces of evidence is also the almost

*) McCafferty & Edmunds (1979) have subdivided the order Ephemeroptera into two suborders, Schistonota (Heptagenioidea, Leptophlebioidea, Ephemerioidea; 13 families) and Pannota (Ephemerelloidea, Caenoidea, Prosopistomatoidea; 6 families) according to construction of hind margin of metanotum and other characters. Some authors (Riek, 1973; McCafferty & Edmunds, 1979) classify Isonychiidae and Coloburiscinae as subfamilies of Oligoneuriidae (Heptagenioidea).

universal retention of a non-functional but practically unmodified gill base («vortex-like structure» by BIRKET-SMITH, 1971) in subimagoes and imagoes of almost all modern families including specialized taxa of the suborder Pannota, such as Tri-corythidae and Caenidae. These structures are distinct also in larvae and subimagoes of *Murphyella* LESTAGE (Siphonuridae: Coloburiscinae), the only genus of mayflies abbranchiate in the larval stage, and have been completely lost together with gills probably in only some genera of the schistonotan families Baetidae and Lepto-phlebiidae. The search for gills in the adult mayflies has shown that the phenomenon of their retention is much more frequent than it could have been a priori expected. Undoubtedly new cases will be found in species of some genera of the superfamilies Heptagenioidea and Ephemeroidea.

Retention of tracheal gills in adults of modern representatives of other insect orders

The occurrence of remnants of tracheal gills in the adult Ephemeroptera must be evaluated jointly with a broader consideration of this phenomenon in other insects. Since no review of this subject more recent than PALMÉN'S (1877) exists, and since textbooks of general entomology and insect morphology and physiology tend to avoid it or to treat it as a mere curiosity occurring in a few genera of Plecoptera only, we also present a short account of the situation obtaining in the other amphibious insect groups.

a) Odonata. The ordinary larvae of Zygoptera and Caloptera (for the conception of this suborder see BELYSHEV & KHARITONOV, 1977) possess appendages of the epiproct and paraprocts which, usually, besides other functions operate as tracheal gills. These three appendages are completely shed off during the larval-imaginal moult and no remnants remain in the adults. However, larvae of two families of Caloptera (Neotropical Polythoridae and Oriental-Palaeartic Euphaeidae [= Epall-agidae]) are provided also with lateral, styli-form, paired abdominal tracheal gills. Lestage (1923a, b) passingly mentioned that remnants of tracheal gills are retained by adult »Calopterygidae«, undoubtedly having had in mind the above families; WESENBERG-LUND (1943) wrote more specifically that the remnants should occur in the genus *Euphaea* SELYS (Euphaeidae). We failed to find any further details in literature; the larval lateral segmental gills have been described in some detail in *Euphaea variegata* (RAMBUR) by RIS (1912) and LIEFETINCK (1962).

The larvae of the suborders Anisozygoptera and Anisoptera breathe by means of rectal tracheal gills («branchial basket») which are capable of not only aquatic but also aerial respiration. In late phases of the life of the last larval instar this respiratory system functions together with the open propneustic tracheal system which eventually replaces the former functionally, still before the larval-imaginal ecdysis (STRAUB, 1943). The intima of rectal gills is cast off during the last ecdysis, and it is either free of larval gill tissues (Aeshnoidea: CALVERT, 1929; WOLF, 1935; STRAUB,

1943), or they are either fully or by their disintegrated parts contained within the shed intima (Libelluloidea: HAGEN, 1880; OGUMA, 1914); PALMÉN'S (1877) assertion that only the aeshnoid mode obtains was erroneous. In any case the six larval rectal pads are replaced by imaginal ones in various ways, be it before the last apolysis or during the first days of adult life. The adult rectal pads may for some time bear spurs of the lost larval structures, but since they are formed only by the imaginal generation of cells, their development was compared by STRAUB (1943) with that of various holometabolan organs. In contrast to rectal pads, the complex tracheal system of larval gills is fully carried over to the adult stage; its considerable reduction and degeneration take place only during imaginal life (STRAUB, 1943).

b) Plecoptera. Tracheal gills are extremely diversified in the larvae of stoneflies. In the suborder Antartoperlaria (for classification adopted see ZWICK, 1974, and also ILLIES, 1960c, 1961, 1962, 1963, 1969 and RIEK, 1970) the most plesiomorphic family Eustheniidae has retained metameric, paired, annulate, leg-like gills on abdominal segments I—IV or I—V (in Stenoperlinae) (ILLIES, 1960c; RIEK, 1970), while the related Diamphipnoidae have subpectinate tufts of filaments on abdominal segments I—IV (ILLIES, 1960c, 1961). The Gripopterygidae (= Abranchioperlidae, Leptoperlidae, Sensillidae) possess a supra-anal rosette of filaments (sometimes retractile or even capable of pulsation - McLELLAN, 1975); only the aquatic larvae of Neotropical *Notoptera* ENDERLEIN (cf. ILLIES, 1960b) and the terrestrial larvae of New Zealand *Rakiuraperla* McLELLAN, *Vesicaperla* McLELLAN and *Holcoperla* McLELLAN (partim; cf. McLELLAN, 1977) are abranchiate. The Austroperlidae (= Penturoperlidae) are highly unique (ILLIES, 1962b, 1969; RIEK, 1970): as gills function 7 to 5, originally annulate, terminal appendages, viz. - elongated cerci (→ shortening and loss of respiratory function), appendages of paraprocts (→ loss of annulation), terminal filament (→ loss of annulation) and a pair of »accessory appendages« between cerci and paraprocts (→ loss of annulation → disappearance); in *Crypturoperla paradoxa* ILLIES, the most advanced species in all the above respects, even the appendages of paraprocts are lacking and there are tufts of gill filaments on the paraprocts and bases of cerci. In the second suborder Arctoperlaria (for data on gills or reviews see e. g. DESPAX, 1949; FRISON, 1935; ILLIES, 1955, 1961; LESTAGE, 1921, 1923a; SCHOENEMUND, 1924; SMITH, 1917) the tracheal gills on abdomen developed as tufts of filaments on segments I—II or I—III are still retained by Pteronarcidae*) and they occur together with thoracic and cervical tufts of filaments (and

*) ILLIES (1961) traced the reduction of segmental occurrence and modification of leg-like abdominal gills into tufts of filaments in the anagenetic series Eustheniidae → Diamphipnoidae → Pteronarcidae. However, the homology of plecopteran tracheopods is doubtful. MILLER (1940) in his embryological study of *Pteronarcys proteus* NEWMAN has conclusively shown that they are not legs; MATSUDA (1976) considered them homologous with the ephemeropteran abdominal gills and hence also with thoracic wings, but KUKALOVA-PECK (1978) rightly pointed out that while the mayfly abdominal gills are situated above the spiracle rudiment (see also BIRKET-SMITH, 1971), those of the stoneflies are always below the spiracle scar. Hence the above homology may apply to the Ephemeroptera but not to the Plecoptera. The homology of the tracheopods of the primitive families of Odonata: Caloptera remains to be investigated; MATSUDA (1976) considers them homologues of thoracic legs.

also - fide PALMÉN, 1877 - with »Analkiemen«?). The same condition should also occur in some Perlodidae (ILLIES, 1961). In the other taxa of Arctoperlaria the gills never occur on proximal abdominal segments; they are developed as a) variously shaped tufts of gill filaments on thorax (sterna, pleura, intersegmental membranes), cervix and terminalia (mostly bases of cerci), b) digitiform gills on thorax (pleura, sterna), cervix and labium, c) retractile, filiform branched anal gills (*Leuctra claasseni* FRISON - FRISON, 1935), d) retractile, segmented coxal gills (*Taeniopteryx* spp. - LAUTERBORN, 1903; LESTAGE, 1921), or the larvae are abbranchiate. The above basic gill types never occur together in the same species, but there exist numerous variations in the topographic arrangement and number of tufts of digitiform gills. First instars in gill-bearing species may be abbranchiate, and tufts of filaments may appear as digitiform gills in ontogeny (ŠAMAL, 1923). The gills are involved not only in respiration, but also in osmoregulation, and they may also perform sensory functions (mechanoreception and chemoreception?) for which they may be equipped not only with the usually trichoid sensilla but also with unique multidigitate types (Eustheniidae - KAPOOR & ZACHARIAH, 1973). Larvae of many Neotropical and New Zealand Griptopterygidae live secondarily in terrestrial habitats together with their adults (cf. ILLIES, 1960a; McLELLAN, 1975, 1977), those of macropterous species of *Aucklandobius* ENDERLEIN being, however, terrestrial in older instars only. The terrestrial larvae may have a closed tracheal system and breathe by means of a fully developed anal rosette of tracheal gills. In terrestrial larvae of other species the gills are reduced or have quite disappeared; in the latter case the larvae breathe by means of an open tracheal system as the adults.

That adult stoneflies may retain larval tracheal gills was first noticed some 135 years ago, but many important problems concerning this phenomenon (most of them raised in the only existing reviews by LESTAGE, 1923a, b) have not yet been answered. Almost no attention has recently been paid to it; symptomatically, it is not mentioned at all in the most recent review of stonefly biology (HYNES, 1976).

The early history of the discovery of tracheal gills in adult Plecoptera may be reviewed here. NEWPORT (1844) found them in N. American *Pteronarcys regalis* NEWMAN (Pteronarcidae); their occurrence was at first considered anomalous (SIEBOLD, 1848), but NEWPORT (1851) confirmed his observation. He thought that the gills may serve for aquatic respiration during oviposition, but EDWARDS (1857) already considered them non-functional. GERSTÄCKER (1873a) described tracheal gills in adults of the Chilean *Diamphipnoa annulata* (BRAUER) (as *D. lichenalis* GERST.; Diamphipnoidae), and similarly to NEWPORT (1851) noticed that they remain tracheate. GERSTÄCKER later (1873b, 1874) successfully looked for these organs also in European Plecoptera; he found them in *Protonemura* sp. (as *Nemoura lateralis* PICTET; Nemouridae), *Perla marginata* (PANZER), and *Dinocras cephalotes* (CURTIS) (Perlidae). Observation of anatomy and behaviour and simple experimentation with live specimens of *Protonemura* sp. strengthened his earlier (1873a) opinion that although the gills of adults are tracheate and similarly built as in the larva, they serve neither aquatic nor aerial respiration, and probably represent only useless remnants of larval organs. GERSTÄCKER (1874) rightly anticipated that more careful examination of adult Ephemeroptera and Trichoptera might reveal the presence of gills also in these orders. PALMÉN (1877) confirmed the retention of tracheal gills by adults of various Nemouridae (cervix) and

Perlidae (thorax, bases of cerci), and, though with some minor errors (occurrence of alleged microbranchiae - cf. LESTAGE, 1923a), provided the first accurate anatomical and developmental observations. By rigorous criticism of NEWPORT's (1851) and GERSTÄCKER's (1874) observations and by his own data he disproved any developmental connections between larval tracheal gills and spiracles, and particularly the idea of the above authors that shedding the gills is necessary for the opening of adult spiracles. He arrived at a remarkable and still basically valid conclusion (p. 34): »Es ist bisher kein Fall sicher bekannt, dass die Tracheenkiemen bei einer Perlide [i. e. Plecoptera - P. Š. & T. S.] abgeworfen werden; bei allen im Larvenstadium Kiemen tragenden Arten, die eingehender untersucht sind, perennieren diese ganz normal beim geschlechtsreifen Thiere, was man bisher nur für seltene Ausnahmen bei einzelnen Arten gehalten hat. Die Larven der Perliden bieten daher als entweder abbranchiate oder perennibranchiate einen auffallende Unterschied von den als caducibranchiaten Larven der Ephemeriden dar.« Most of the subsequent observations and generalizations published on various taxa of Plecoptera from all over the world in the period 1877—1923 (at least SMITH's, 1917, exploitation of adult gills for the taxonomy of North American Perlodidae should be noted) were summarized by LESTAGE (1923a, b).

Modern plecopterists (e. g. FRISON, 1935; DESPAX, 1949) seem to agree with PALMÉN's (1877) assertion that Plecoptera are perennibranchiate. Indeed, abdominal metameric gills, both digitiform and multifilamentose thoracic/cervical/labial gills as well as coxal segmented gills have been found in adults of practically all families in which occur larvae possessing gills of the above types, and perennibranchiality is probably universal in the taxa concerned.

The occurrence of these kinds of gills in adult stone-flies has been reported in Antarctoperlaria for Eustheniidae by TILLYARD (1921a), HESLON (1935) and ILLIES (1960c), for Diamphipnoidae by GERSTÄCKER (1873a), TILLYARD (1921b) and ILLIES (1960c); in Arctoperlaria for Pteronarcidae by NEWPORT (1844, 1851), HAGEN (1877), SMITH (1917) and FRISON (1935), for Perlodidae by SMITH (1917) and FRISON (1935), for Perlidae by GERSTÄCKER (1873b, 1874), PALMÉN (1977) and FRISON (1935), for Nemouridae by GERSTÄCKER (1873b, 1874), PALMÉN (1877), KEMPNY (1898), LESTAGE (1923a, b) and EGGERT (1937), for Taeniopterygidae by LAUTERBORN (1903), LESTAGE (1921) and FRISON (1935). This account only illustrates the wide occurrence of this phenomenon; we have not attempted to cover all pertinent literature and some important sources have remained unavailable to us. We failed to find any record of retention of the digitiform thoracic gills by adult Peltoperlidae, but also found no statement to the contrary. LESTAGE (1923a, b) emphasized the absence of, or rather his inability to find, any traces of gills in adults of some Perlidae with branchiate larvae; the latter was probably the case since, as many authors noted, the gills of adults are often distinct only on fresh specimens.

However, perennibranchiality probably does not concern (at least not universally) various types of terminal abdominal gills. In Antarctoperlaria the annulate terminal appendages (or their distal parts with respiratory function) of Austroperlidae are cast off at the last moult (ILLIES, 1960b), and we have not found any record of retention of the conspicuous supra-anal rosette by adult Griptopterygidae; the same applies to similarly situated tufts of filaments in various Arctoperlaria and to retractile anal gills of *Leuctra claasseni* FRISON. Only PALMÉN (1877) reported that the terminal gills of some Perlidae are carried over to the adult stage; they collapse, shrink, and remain hidden by terminalia.

Summarizing the data of the authors quoted above, the gills of the adult Plecoptera may be characterized, as follows: With the exception of some of the gills situated terminally on the abdomen (loss due to considerable reconstruction of terminalia at

the last moult?) they are perennibranchiate, and although they are slightly to considerably smaller («reduced», «vestigial») than those of the larvae, they retain the larval shape and all their cuticular, tracheal and sensory structures (PALMÉN, 1877; EGGERT, 1937). The gills of teneral adults are tumescent; however, a fast to gradual and to a varying degree proceeding degeneration takes place during the early or later phases of adult life (this apparently never happens in some species or some individuals). The gills dry up, shrink and shrivel, so that their components and eventually all gills become almost indiscernible; some groups are probably more (e. g. Perlidae), some less (e. g. Nemouridae, Pteronarcidae) prone to desiccation. The coxal gills of Taeniopterygidae are probably eventually retracted and are represented by scars or tubercles only.

LESTAGE (1923a, b) criticized various controversial statements and inconsistencies found in literature, and posed some important questions. Do all individuals of the same species retain their gills? In those which do, are the gills equally developed? Does degeneration of gills proceed by the same way and to the same degree in all individuals? These questions were also inspired by his observations of *Amphinemura sulcicollis* (STEPHENS) (as *cinerea* (OLIVIER)), *Protonemura humeralis* (PICTET) and *P. meyeri* (PICTET) (all Nemouridae). He claimed that only 6—10 % of adults retained the gills, and that in comparison with larvae were the gills reduced in various degrees which roughly corresponded to the observed sequel of degeneration during the adult life. However, EGGERT's (1937) observations of *Protonemura nitida* (PICTET) were different; all adults retained tumescent gills, and their anatomy (tracheal supply, nerves leading to trichoid sensilla, adipose tissue with haemolymph lacunae) was larval. All modern authors agree that adult gills of plecopterans are non-functional (old hypotheses on their possible function were based on insufficient knowledge of plecopteran biology and are mentioned by GERSTÄCKER, 1874, and LESTAGE, 1923a, b). EGGERT's (1937) data (as well as the existence of some terrestrial larvae of gripterygids breathing only by tracheal gills) suggest that in air with sufficiently high relative humidity the gills of some species could engage in cutaneous respiration. Since the adult gills always coexist with an open tracheal system, such a function is superfluous; ligatures of gills (EGGERT, 1937) have not impaired the lives of affected adults.

We offer the following hypothesis to explain the situation. The adult stoneflies almost universally retain the larval gills and their organization; since the adult gills are covered with cuticle thinner than that of intersegmental membranes (EGGERT, 1937), they must dry up in atmosphere of a lower relative humidity than that of the internal body environment. Any mechanism protecting their turgor would be selectively disadvantageous, since it would increase the loss of water and could lead to eventual desiccation of the whole individual. However, the onset of degeneration of no more needed gills, its rapidity, course, ultimate stage, and whether the process takes place at all depend on interaction of factors concerning the phylogenetic history of a species (anatomical and physiological properties of gills; inherited behaviour and ecological preferences), life-history of an individual (accidental encounters

with atmosphere of low r. h.; age, increasing likelihood of such encounters) and climate (microclimate) of an area, locality and habitat in which a species (individual) lives and on its unpredictable changes. Thus a broad spectrum of taxonomic, geographical and individual variation in the degree of adult degeneration of gills can be expected. However, both observational and experimental corroboration of this hypothesis on model species is needed; it would also answer the questions posed by Lestage (1923 a, b).

c) Phasmatodea. Interpretation of a basi-abdominal lobulate organ in adults of a Bornean species *Cotylosoma dipneusticum* WOOD-MASON (Phasmatidae) as tracheal gills and, consequently, assumption of an amphibious life of this species (WOOD-MASON, 1878) apparently belongs in the realm of phantasy. However, LESTAGE (1923a, b) mentioned the presence of tracheal gills in adults of both *Cotylosoma* WOOD-MASON and a Neotropical genus *Prisopus* LATREILLE (Pseudophasmatidae) and regarded both genera as »dulcicoles«. All this was repeated by WESENBERG-LUND (1943) who also added some details on the supposed amphibious life of the latter genus. No report about the improbable existence of aquatic or amphibious Phasmatodea appears in modern literature, and the alleged cases are not mentioned by BEDFORD (1978).

d) Megaloptera. It would seem likely that the larval abdominal paired lateral segmental gills could be retained in adults of this most primitive holometabolan order. However, in an externally visible form they are not. The major features of the metamorphosis of gills were already noted by PALMÉN (1877), and the gradual »Abbau« of gills during the larval-pupal and pupal-imaginal moults of *Sialis lutaria* (L.) was studied in detail by OCHSÉ (1944). The Abbau starts with retraction of the apex of the trachea branchialis, is followed by proximally progressing apolysis and retraction of the gill content into the abdominal cavity, accompanied by phagocytic destruction of larval gill tissues. The gills are shed during the larval-pupal ecdysis, and only non-articulated stumps indicate their original position in the pupa; inside, then only autolytic destruction of the original gill content is completed. The adult possesses no external remnants of abdominal gills; however, the trachea branchialis has not been completely destroyed. From the pharate pupa onwards its matrix and intima are condensed into a gradually diminishing petiolate sac suspended from the respective spiracular atrium; this internal sac is carried over into the adult stage and its intima is never cast off, so that remnants of the larval intima are found even in the adult. Although no pupal intima is formed, the secretory activity of the surviving matrix cells is resumed at pupal-adult moult and irregular pieces of imaginal intima are formed in this reduced and obviously non-functional organ.

e) Trichoptera. Larvae and pupae of most of the case-making species and some non-case-making ones are provided with variously situated abdominal (in some species also thoracic) tracheal gills; they may be filamentose, lobulate, digitiform, single, or arranged in tufts; sometimes they are also paired, lateral and segmental. The cases of retention of these gills in adults are apparently common, but they

have been rarely mentioned. Although discovered by PALMÉN (1877) in several genera, they remained unknown even to LESTAGE (1923a, b).

HANDLIRSCH & BEIER (1936 : 1499) laconically stated on the abdomen of adults: »Die Pleuralhäute der ersten 8 Segmente sind bei allen Trichopteren mit Ausnahme der Odontoceriden mit kleinen, unscheinbaren, nur am frischen Material erkennbaren und im Leben wohl funktionslosen Kiemenanhängen ausgestattet«*). The opinion of WESENBERG-LUND (1943) is the same; he also summarized the relationship between larval and pupal tracheal gills: the gills are in a somewhat modified form carried over to the pupa, rarely are they completely lost (e. g. in *Rhyacophila* species), and sometimes, in some of the groups with abbranchiate compodeiform larvae, they may develop only in the pupa (e. g. in the Polycentropidae). According to PALMÉN (1877), gills are not cast off by the pupa of *Rhyacophila vulgaris* PICTET, but retracted.

A detailed investigation of the metamorphosis of tracheal gills in *Hydropsyche* species was carried out by HALLER (1948). The pupa retains a slightly reduced system of larval tufts of filamentose gills (the meso- and metathoracic tufts and inner rows of abdominal tufts are lost) and develops its own system of latero-abdominal lobe-shaped gills from larval Anlagen which, however, start to grow already at the onset of the prepupal period, still before the larval-pupal apolysis. The fresh adult retains both larval and pupal systems of tracheal gills, but both are deciduous: »Wenige Stunden nach dem Schlüpfen, wenn sich das Abdomen dunkel gefärbt hat, sind die Kiemen eingetrocknet. Beide Kiemenarten verschwinden somit durch Austrocknung, ohne das eigentliche Abbauvorgänge stattgefunden hätten oder dass sie durch eine Häutung abgestossen worden wären.« A similar situation was noted by PALMÉN (1877); both authors concluded that no respiratory function of adult gills is possible.

f) Many of the amphibious species of the orders Neuroptera, Coleoptera, Lepidoptera and Diptera possess variously situated (mostly abdominal) filamentose or digitiform, or rarely paired, lateral, segmental and leg-like (e. g. Gyrinidae) tracheal gills in their aquatic juvenile stages; however, no case of their retention in adults is known to us. PALMÉN (1877) thought that the gills of larvae of branchiate aquatic Lepidoptera (he mentioned particularly the pyralid *Paraponyx stratiotata* (L.)) would possibly behave similarly to those of Sialidae and Rhyacophilidae, and that they would not be cast off but retracted and their remnants carried over to the adult stage. He expected a similar situation also in the Sisyridae and Gyrinidae.

*) This is certainly an overstatement. Gills lost in some taxa in the pupal stage would have to develop again in adults, and the gills of adults would be purely imaginal organs in groups with all juvenile stages abbranchiate. This is hardly believable, and a review of the occurrence of adult gills in caddisflies is urgently needed.

1. Possible functions of tracheal gills in adults

Our insufficient knowledge of gill retention in the calopterous Odonata prevents us from discussing it. The adult vestiges of gills of the anisopterous Odonata and Megaloptera are in such an advanced state of Abbau that they are undoubtedly non-functional.

a) Respiration. The adult remnants of tracheal gills always coexist with normally functioning open tracheal and spiracular systems, and the fully terrestrial adults of the gill-bearing species do not bionomically differ from their abbranchiate relatives. Hence any respiratory function of tracheal gills during adult life is unnecessary and, if existing, superfluous. The gills of Trichoptera and some Plecoptera (see also the final part of the review of gill occurrence in the latter order) quickly dry up and can take part in aerial respiration only in the early stages of adult life. The always atracheate remnants of both abdominal and accessory gills in the subimagos and imagoes of Ephemeroptera have not been observed in live individuals and it is unknown whether they retain their tumescence during the short imaginal life. The adult gills of these orders (whether tracheate or atracheate) probably can take part in the exchange of gases while tumescent due to their thin cuticle, but their role is surely unimportant and greatly quantitatively and temporarily limited. However, we do not doubt that the tracheal gills of those Plecoptera which retain their tumescence all the time and are provided with unmodified tracheal and haemolymph supply (cf. EGGERT, 1937) are anatomically fully capable of both aquatic and aerial respiration; clear indirect evidence of the latter is the terrestrial life of some apneustic gripterygid larvae breathing only by means of their anal rosette of tracheal gills. Although the contribution of tracheal gills to aerial respiration is impossible to estimate without experimental evidence, their respiratory function is surely not essential, as shown by EGGERT'S (1937) ligature experiments. The females of most ephemeropterans and plecopterans and a few trichopterans come in contact with water (or even submerge their abdomen) during oviposition, but their behaviour does not require and does not enable any aquatic respiration.* Females of many trichopterans walk or swim under the water for oviposition; it is unlikely that tra-

*) The adults of *Zapada cinctipes* (BANKS) (Plecoptera, Nemouridae) living in severe and fluctuating climatic conditions of Sierra Nevada Mts. in California were reported (TOZER, 1979: Nature, 281: 566—567) to thermoregulate behaviourally by entering the water at subzero night temperatures; the adults are partially enveloped in a film of air and regularly ascend to air pockets below the ice within which they are presumed to obtain surface oxygen. Nevertheless, TOZER (l. c.) suggests that the two pairs of cervical gills of this species may enhance underwater oxygen diffusion. The apterous species *Capnia lacustra* JEWETT (Plecoptera, Capniidae) living in a nearby Lake Tahoe is fully aquatic and devoid of gills in both larval and adult stages (JEWETT, 1963: Science, 139: 484—485); its respiration is probably cutaneous. It seems therefore improbable that perennibranchiality would be a necessary preadaptation for rare secondary returns of adult stoneflies to the aquatic environment.

cheal gills would be used, since spiracular plastron respiration probably takes place, or the body may bear a large air bubble under the compressed wing, similarly as in some subaquatically ovipositing mayflies (*Baetis* spp.).

b) Water exchange. Active intake of water through remnants of tracheal gills is unlikely; no presence of a special absorption epithelium (like that of thysanuran vesicles) has been reported and its development only after the termination of the aquatic phase of development is improbable and unnecessary, since adults of the species involved either can and do drink orally (Plecoptera, Trichoptera) and can easily reach liquid water, or are short-lived (Ephemeroptera, particularly subimagos) and water loss (amounting up to 25 % of body weight) rather than gain is an essential prerequisite of their further development (cf. LANDA, 1969). The presence of gill remnants also does not increase the hazard of excessive water loss. Adults of the species involved generally live in humid microhabitats and/or have easy access to them and can thus easily regulate their water loss by behavioural means, even if their gill remnants would be permanently tumescent. However, in most species the gills probably dry up in dry atmosphere; the process is fast, the bases of gills small, and the shrivelling of gill cuticle probably compensates for its thinness, so that it is dubious whether the evaporation quotient of the shrunken gill is higher than that of unmodified and always only slightly sclerotized abdominal cuticle. It is therefore improbable that adult gills would play a significant role in the maintenance of proper water balance.

c) Sensory function. Since the sensilla and innervation of gills are retained in at least some branchiate species of adults (cf. data on Plecoptera by EGGERT, 1937) it is probable that while tumescent the adult gills could take part in mechanoreception and chemoreception; because of non-sclerotization and thinness of their cuticle they could also function as barometric and hygrometric organs. The whole gill remnant may possibly function as a hygroreceptor in species where it dries up: the proprioceptive stimuli caused by its deformation during desiccation may possibly play a role in the regulation of behaviour and in the change of hygro taxis. However, any experimental evidence of the sensory function of adult gills is lacking and it is probable that in atracheate species the nerves have been retracted together with the associated tracheae during metamorphosis.

Hence it seems that the gills are either non-functional during the adult life or that their possible functions are superfluous, unessential or doubtful. Basically the same conclusion was also reached by PALMÉN (1877) and LESTAGE (1923a, b). If any function at all is performed by the adult gill, it can be carried out only while it is in a tumescent state or just drying up. However, with non-deciduous gills it is apparently unknown whether their deformation owing to desiccation is reversible or irreversible.

2. Possible function of gills during metamorphosis

a) **Respiration.** The last larvae of Odonata, Plecoptera and Megaloptera always leave water prior to the larval/adult or larval/pupal ecdysis and at the same time they start breathing with an open (usually hemipneustic) tracheal system. Moreover, a layer of air is eventually distributed below the apolysed larval cuticle and, consequently, there is no need for the already terrestrial pharate adults or pupae to use larval gills for respiration. Another situation obtains in Trichoptera. There the pharate adult is fully aquatic and has to be considerably active while cutting its way out of the pupal case or cell and swimming to the surface where eclosion takes place. Although a layer of air is then already present between the pupal cuticle and cuticle of the pharate adult which is already capable of breathing with open spiracles, it is possible that diffusion through the fine cuticle of pupal/pharate adult gills provides an additional and for some species necessary source of oxygen for the short period of intensive imaginal aquatic activity.

Eclosion of the subimagos of Ephemeroptera takes place mostly on water surface (also in most of the perennibranchial species) or, more rarely, only after the last larva has emerged the front part of its body out of water (Coloburiscinae of the perennibranchial species); spiracles of the pharate subimago which never exerts any remarkable activity are always open and there is also an air layer between the larval and subimaginal cuticles. Therefore it seems unlikely that respiration through adult gills is needed during metamorphosis, particularly when a rather mosaic-like distribution of perennibranchiality among mayflies is taken into account. However, a continuation of the respiratory function of adult gills is very well conceivable for such mayflies as *Palingenia* species: they are large, and a continuously high rate of oxygen supply may be necessary because of a small surface/volume ratio; also their metamorphosis is abbreviated and the duration of the subimaginal stage is very short, the imaginal cuticle being already present under the cuticle of the pharate subimago. This may enhance the necessity of intensive oxygen supply and result in relatively good retention of gills simply because there is no time to get completely rid of larval organs during the larval/subimaginal apolysis.

b) **General facilitation of metamorphosis.** A smooth transition from the aquatic to terrestrial environment during the metamorphosis of amphibiotic orders is assisted by numerous mechanisms (WESENBERG-LUND, 1943: 613 ff.); the respiratory function of adult gills is not among them (with a possible but unproven exception of caddisflies and *Palingenia*-like mayflies). However, it could be argued that possession of adult gills is a selectively neutral and in some taxa and under certain conditions probably advantageous character, and that selection would therefore promote its development*) since, anyway, perennibranchiality makes metamorphosis simpler

*) By making the tissue of tracheal gills relatively insensitive to changes in the juvenile hormone titre - this is what »neoteny« offered as an explanation of perennibranchiality by Lestage (1923a) would really mean, since the species involved do not show an overall retention of larval features corresponding to an increased JH titre or premature onset of metamorphosis when compared with their relatives.

and shorter. We believe that this adaptive explanation is also incorrect for the following reasons:

a) The distribution of perennibranchiality is too irregular.

b) The other groups of amphibiotic insects execute by various ontogenetic processes (see the review of Odonata and Megaloptera) an efficient Abbau of tracheal gills or simply cast them off.

c) Adults of the perennibranchiate taxa generally belong to non-feeders or their food is poor in protein content; hence, from the energy budget point of view it would seem more advantageous for them to reconstruct and use the gill tissues rather than to retain the gill and to maintain a useless organ which eventually dries up or falls off (the caducibranchiality of the zygopteran gill-fin might also seem disadvantageous from this point of view; however, the organ also functions as a deciduous protective bait during larval life).

d) Generally, the larval organs of pterygotes are not taken over to the adult stage unless really neotenuous situations are involved; those of holometabolans are reconstructed or destroyed and the same is true for a few special juvenile organs of some non-aquatic exopterygotes (e. g. adhesive organs of some Sternorrhyncha; glandular macrotrichia and their processes in many Heteroptera). The only exception to this rule we can recall is the almost universal retention of the cuticular structures of larval dorso-abdominal glands by the adult Heteroptera which is in some cases also accompanied by retention of functional gland tissues; this never properly reviewed situation is in many respects a phenomenon similar to perennibranchiality.

Since we have not found a sufficiently valid universal adaptive basis for modern perennibranchiality and since an idea of a many times repeated evolution of a non-functional character (as implied by almost all authors who tackled the subject and wrote about »retention of juvenile structures«) is clearly unacceptable, we have to look for the explanation of this phenomenon in the past history of insects.

3. Phylogenetic implications

The adult gills bear all the marks of vestigial organs: their taxonomic distribution is irregular but largely associated with primitive orders and their primitive subgroups; they exhibit an increased individual variability; their size decreases during the final stages of development (note particularly the two adult instars of the Ephemeroptera!), partly possibly due to their negatively allometric growth but largely because of compensation of body material (two principles particularly emphasized by RENSCH, 1959: 225); there is no clear adaptive explanation of their presence (they are largely »useless«). Once we conclude that they are vestigial organs we also have to infer that a) their presence in modern adults of any of the orders involved is plesiomorphic, b) they were inherited from branchiate adult ancestors and then reduced, and c) they were present in a functional state in complete ancestral ontogenies, i. e. in both juveniles and adults. These inferences have far-reaching phylogenetic implications which will be only cursorily examined below.

The fossil record does not yet include any ancestral pterygotes («propterygotes» further on) which must have already lived in the Late Devonian, since numerous pterygote orders suddenly appeared in the Carboniferous. The oldest fossils (CROWSON et al., 1967; HENNIG, 1969; RODENDORF, 1962) of the major insect groups are from the following periods: Monura - Late Carboniferous; Thysanura - Late Triassic; Palaeoptera - Early or Middle Carboniferous; Plecoptera - Early Permian; Polyneoptera s. str. (= Paurometabola Hennig) - Early Carboniferous (Namur); Paraneoptera - Early Permian; Holometabola - Late Carboniferous (*Metropator pusillus* HANDLIRSCH /? Mecoptera/ and *Fatjanoptera mnemonica* MARTYNOVA /? Raphidioptera/) or Early Permian. The perennibranchiate orders include the only two extant palaeopteran orders, the Ephemeroptera and Odonata, the most primitive extant neopteran order - the Plecoptera, and a very primitive holometabolan order, the Trichoptera (the earliest fossil: *Microptysma sibiricum* MARTYNOVA of Early Permian); hence all the major pterygote groups known from the Carboniferous are represented (for Polyneoptera s. str. and Paraneoptera see below). It is then reasonable to assume that the symplesiomorphic characters of these orders were also shared by their common propterygote ancestor.

Almost universally amphibious development*) is characteristic of only five extant insect orders, and perennibranchiate species occur in four of them; probably also the most plesiomorphic holometabolans, the Megaloptera, would be on the list of perennibranchials if their aquatic phase of ontogeny were not relatively shorter than that of the Ephemeroptera, calopterous Odonata, Plecoptera and Trichoptera. If all the latter groups had perennibranchiate ancestors, we may rightfully ask whether the perennibranchiality of tracheal gills (but not necessarily any particular modern gill type) is also their common symplesiomorphy, and, because of their cladistically strategic position, also a character possessed by the propterygotes. Since the presence of gills undoubtedly is and was associated with aquatic or at least ontogenetically amphibious existence, this question inevitably leads to the problem of major shifts of environment during the early evolution of pterygotes. A pertinent motto linking perennibranchiality with this complex problem is provided by REMANE's (1952: 307) generalization that »wechselt ein Tier seinen Lebensraum, so bleiben die Merkmale des ursprünglichen Lebensformtyps oder Funktionstyps oft länger erhalten als den ökologischen Anforderungen des neuen Lebensraumes entspricht«.

Leaving aside such basic problems as the acquisition of tagmatization, oligopody and hexapedous gait, divergence of thysanurans (& monurans?) and pterygotes, acquisition and further evolution of pro-wings and development of metamorphosis, and concentrating only on aspects related to respiration, we may summarize the major current opinions on early environmental shifts, as follows:

A) Pterygotes had aquatic atracheate ancestors which had to become fully terrestrial to acquire the tracheal system and spiracles. Transition to terrestrial life was achieved through an intermediate period of occasional, possibly nocturnal visits to land (SMART, 1971) or through a long period of edaphic life (GILYAROV, 1949). Juveniles of ontogenetically amphibious orders gradually returned to aquatic life; evidence of

*) The term »amphibious« (meaning living both on land and in water) is ambiguous; in further discussion we shall distinguish between ontogenetically amphibious (i. e. with aquatic juveniles and terrestrial adults, meaning usual in entomology) and eamphibious (being able to live in both environments at the same time and in the same stage).

its secondary character is seen for instance in the presence of rudimentary spiracles in the juveniles (BIRKET-SMITH, 1971). This is an orthodox theory (accepted also by WOOTTON, 1972), and even the usually skeptical HENNIG (1969: 125) took this course of events for granted and did not attempt to disprove the alternatives.

B) The atracheate aquatic propterygotes became ontogenetically amphibious and evolved tracheae at first in their older terrestrial instars. The development of the tracheal system was later accelerated: the tracheae also appeared in younger instars and penetrated into the gills of juveniles (RIEK, 1971). The original terrestrial habitat is - probably correctly - looked for in the emergent vegetation of the earliest terrestrial plants (Psilophyta) growing in swamps in extremely humid air (MAMAEV, 1976). HENNIG (1969: 126) formulated a hypothesis (entirely improbable in his opinion) that full terrestriality could have been achieved by ever earlier transition to terrestriality in ontogeny.

C) KUKALOVA-PECK (1978), in her apt survey and original synthesis of ideas concerning the origin of wings, is deliberately vague about environmental shifts but she basically suggests a sequence aquatic atracheate ancestor → tracheate terrestrial or euamphibious pterygote with homologous thoracic and abdominal pro-wings → ontogenetically amphibious pterygote. She hesitates whether the pro-wings evolved during the original aquatic stage (possibly as gill covers) or during the second, terrestrial/euamphibious stage (possibly as protective flaps for spiracles without closing apparatus), but she definitely requires the latter stage for the appearance of the tracheal system and the following ontogenetically amphibious stage for the promotion of wing evolution through their function in the aquatic juveniles. She asserts that the earliest known fossil juveniles from her second stage were terrestrial (even Ephemeroptera!), without adaptations for aquatic locomotion.

Which of the above models is compatible with our inference that the ancestors of probably all modern ontogenetically amphibious orders were perennibranchiate? Certainly not the orthodox model A (aquatic → terrestrial → ontogenetically amphibious), since it denies ancestral perennibranchiality any possible function unless we assume that already then it was non-adaptive and maintained only by the mechanism of then still probable ametabolic development. Moreover, a satisfactory explanation why the secondary reversal to aquatic life occurred, why it was so universal, why it always resulted in apneustic respiration and in the development of tracheal gills, and why it concerned only the primitive modern orders of the Palaeoptera, Perlodea and Holometabola, has never been offered with this model. *) WOOTTON (1972)

*) All the modern aquatic (some Heteroptera), euamphibious (some Mallophaga, Echinophthiridae, some Heteroptera) and ontogenetically amphibious (some Cercopoidea) Paraneoptera have undoubtedly evolved from terrestrial ancestors; they never evolved any kind of gills, have always retained the open tracheal system, or have simple cutaneous respiration in early instars. Also all modern orders of Polyneoptera s. str. are fully terrestrial, and a few species of Blattodea, Phasmatodea, Ensifera and Caelifera, secondarily semiaquatic or temporarily entering aquatic environment (cf. WESENBERG-LUND, 1943) did not have to evolve any aquatic respiratory organs.

attempted to overcome this difficulty by assuming that »the survival of these orders whose adult structure is relatively primitive may result from the successful exploitation by their larvae of the possibilities of fresh water, where rather few higher groups are competing«. WOOTTON's main argument is the fossil record: as he reviewed the matter, of all the extinct Palaeozoic insect orders only the family Lemmatophoridae* is known to have aquatic larvae. We believe that the palaeoentomological fossil record is too incomplete and unreliable to allow such a conclusion. The less sclerotized aquatic larvae are less likely to become fossilized than the more sclerotized terrestrial adults, the delicate tracheal gills are still less likely to be preserved, and in crawling benthic predators (regarded by WOOTTON, 1972 as the first insect pioneers of freshwater ecosystems) it is hardly possible to expect an occurrence of features that would enable us to recognize their aquatic habit from their structures preserved in fossil remnants. On the other hand, the mere presence of lateral paired abdominal appendages (as in larval Lemmatophoridae) in the shape of segmental pro-wings is not a sufficient evidence of their aquatic life within the paradigm of KUKALOVA-PECK's (1978) theory. However, it is probably significant that the Lemmatophoridae are phenetically acceptable as belonging to a group directly ancestral to the Plecoptera (cf. CARPENTER, 1935; HENNIG, 1969), and that the Plecoptera possibly are a sister-group of the Holometabola (cf. YEMEL'YANOV, 1977).

The model B (aquatic → ontogenetically amphibious) is simpler and compatible with the cladistic position of modern ontogenetically amphibious orders. However, it requires a) retention of atracheate gills of the aquatic ancestor by the older terrestrial instars of perennibranchiate species, b) development of tracheal system and its penetration into non-functional gills first in these terrestrial instars, and c) slow appearance of these characters ever earlier in the aquatic juveniles. These processes are incompatible: a) requires ametabolous development, b) amounts almost to the development of metamorphosis, and c) to its at least partial suppression.

Model C (aquatic → terrestrial or euamphibious → ontogenetically amphibious) presumes the existence of an ontogenetically amphibious grade in the ancestry of all pterygotes. Consequently, it seems implausible, assuming that its second phase would be terrestrial: the postulated environmental shifts are unnecessarily complicated and most of the objections raised against model A apply. However, the sequence of grades »aquatic → euamphibious → ontogenetically amphibious« is most parsimonious as far as the environmental shifts are concerned and also fully corresponds with the presumed symplesiomorphic perennibranchiality of the ancestral pterygotes.

*) Classified as a single family of the order † Protoperlaria by CARPENTER (1935), in broadly conceived † Paraplecoptera by SHAROV in RODENDORF (1962) and by CROWSON et al. (1967), and in still more broadly conceived † Protorthoptera by CARPENTER (1966) and WOOTTON (1972).

We may visualize the aquatic propterygotes as branchiate, tracheate,*) prespiraculate, polypodous and ametabolous creatures possibly already possessing thoracic and abdominal pro-wings. Only a minor perfection of the spiracular system would enable such a versatile insect to turn to euamphibious life in a humid terrestrial environment as soon as it becomes available and inhabitable - the insects were equipped for respiration in both aquatic and terrestrial environments which at that time differed less sharply than nowadays. Perennibranchiality was then functional, was maintained by selection and realized by ametabolous development.

Further environmental history of the pterygotes must have been closely connected with the perfection of wings, and we cannot discuss it here. We only wish to point out that transition to the ontogenetically amphibious life was probably enforced by increasing differences between forces of selection operating in the two environments, and that the duality of selection pressure might have been a key factor in the evolution of metamorphosis. If the turn to the ontogenetically amphibious life was universal, as KUKALOVA-PECK (1978) assumes, then the hypothesis outlined above would explain why the primitive groups of most of the major pterygote lineages retained this type of development (symplesiomorphy) and why perennibranchiality is proper to at least some of their species (a relic of symplesiomorphy from the euamphibiotic and ametabolic phase). However, it seems improbable that the early history of environmental shifts in insect phylogeny would be so straightforward. It seems possible that some lineages proceeded from the euamphibiotic direct to fully terrestrial life; this may apply to the palaeodictyopteran orders of the Palaeoptera, and to the Polyneoptera s. str. (= Paurometabola) and Paraneoptera of the Neoptera. Reassessment of the classification and cladistic affinities of various Palaeozoic juveniles regarded as terrestrial ancestors of modern ontogenetically amphibious orders by KUKALOVA-PECK (1978), and particularly a definite establishment of their macrohabitats is of primary importance in this respect.

In any case, the adult tracheal gills are probably »living fossils« among the organs of modern adult pterygotes. Their development apparently was so deeply rooted in the epigenotypes of the ancestors of modern perennibranchiate species that it has not been entirely suppressed by metamorphosis and long non-functionality during

*) The tracheal system of propterygotes need not have evolved in terrestrial environment. The course of events might have been, as follows: a) diminution of the size of the aquatic pre-insect resulting in reduction of its circulatory system (and eventually also of previously present gills); b) increase in its size accompanied by a necessary strengthening of the cuticle for attachment of stronger muscles resulting in insufficiency of the cutaneous respiration and development (or increase in size) of gills (for a review of ideas associating evolution and function of gills with that of pro-wings see Kukalova-Peck, 1978); c) further increase in size necessitating the evolution of tracheae forming an efficient system for oxygen transportation from gills to body tissues and for the fastening of inner organs (in this stage permanently apneustic spiracles would function only as sites of embryonic or early postembryonic invagination of tracheal tissues and of pulling out the tracheal intima after each moult). Both prespiracles and the tracheal system would then be important and immediately ready preadaptations for a shift of propterygotes to at least partially terrestrial life. Most of the modern larvae of the ontogenetically amphibious orders are provided with tracheal gills, a well developed tracheal system and rudimental spiracles, and thus correspond to the suggested anagenetic stage c).

the more than 300 million years of the terrestrial existence of adult pterygotes. Hence, perennibranchiality is not merely an interesting aberrant phenomenon, but a remnant of a memorable and still largely unknown past of insects, and probably also a partial key to it.

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