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**GYNANDROMORPHISM, INTERSEXUALITY AND TERATOLOGY OF EXTERNAL  
GENITALIA IN THE ORDER EPHEMEROPTERA**

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Received February 15, 1980

**Abstract:** Literary data and data obtained by the study of more than 20 specimens showing gynandromorphism, intersexuality or external genitalia teratology are summarized. While head and thorax show the bilateral type of gynandromorphism, abdomen exhibits a mosaic-like distribution of male and female portions; exceptions are described in detail. Genetically conditioned gynandromorphism is considered to be either spontaneous (early loss of an X chromosome) or connected with polyspermy and starting of parthenogenetic embryogenesis. Gynanders are most frequent in the families Baetidae, Heptageniidae and Leptophlebiidae (large number of species, high degree of sexual dimorphism). Intersexuality is caused by parasitic worms of the family Mermithidae. Parasitization is connected with the masculinization of females (10–40%) and at least partial castation (75–100%). Intersexes occur only in the family Baetidae. External genitalia teratology is conditioned either genetically (occurrence of supernumerary forceps on sternum VIII) or by a relatively very high ability to regenerate loss of genital or even 1-2 pregenital abdominal segments in larval stage.

Mayfly specimens (mostly adults or subimagos) having both male and female secondary sexual characters were first mentioned many years ago (Lestage, 1922; Bengtsson, 1928 and others). Since then several tens of such specimens have been described in 5 mayfly families. These individuals called “anomalous or monstrose specimens”, “hermaphrodites”, “intersexes”, “sexual mosaics”, “gynanders or gynandromorphs” etc. actually represent three categories of departures in the arrangement of secondary as well as primary sexual characters: true gynandromorphism (male and female parts of body normally developed, only exceptionally reduced in size, evenly or unevenly distributed), intersexuality (male and/or female parts of body intermedially developed, always unevenly distributed) and external genitalia teratology (deformations or unusual location of forceps and penis lobes).

Previous publications mostly represent descriptive morphological studies of these phenomena. Only little attention has been paid to factors causing gynandromorphism and intersexuality and to a relatively higher occurrence of these specimens in some families. In the following paragraphs morphological characteristics of these specimens are summarized and an attempt to analyze the nature, causes and distribution of these phenomena within the taxonomic groups is made.

**MATERIALS AND METHODS**

The following specimens showing atypical distribution of male and/or female secondary sexual characters or atypical arrangement of external genitalia were studied:

*Baetis alpinus* (Pictet), adult: Czechoslovakia, South Bohemia, Vltava riv., Ovesná, 23. x. 1953 leg. O. Winkler (specimen No. 1); *B. alpinus* (Pictet), adult: Czechoslovakia, North Bohemia, Teplá riv., Teplička, 12. vi. 1955 leg. V. Landa (No. 2); *B. fuscatus* (L.), adult: without any data, leg. M. Straškraba (No. 3); *B. fuscatus* (L.), adult: without any data, leg. M. Straškraba (No. 4); *B. fuscatus* (L.), adult: Czechoslovakia, South Bohemia, Lužnice riv., Bechyně, 4. viii. 1973

leg. T. Soldán (No. 5); *B. fuscatus* (L.), adult: Czechoslovakia, Central Bohemia, Sázava riv., Stříbrná Skalice, 25. ix. 1976 leg. T. Soldán (No. 6); *B. muticus* (L.), adult: Czechoslovakia, Central Bohemia, Bojovský brook, Měchenice, 23. v. 1960 leg. V. Landa (No. 7); *B. muticus* (L.), larva: Czechoslovakia, Central Bohemia, Zahořanský brook, Davle-Libřice, 5. xi. 1977 leg. T. Soldán (No. 8); *B. rhodani* (Pictet), adult: Czechoslovakia, South Moravia, brook, Chřibská Kamenice, 28. viii. 1957 leg. V. Landa (No. 9); *B. rhodani* (Pictet), 35 larvae: Czechoslovakia, Central Bohemia, Zahořanský brook, Davle-Libřice, 5. — 19. xi. 1977 leg. T. Soldán (No. 10); *B. rhodani* (Pictet), subimago, 2 adults, same data (No. 11); *B. vernus* (Curt.), subimago: Czechoslovakia, Central Bohemia, brook, Obořiště, 20. vi. 1960 leg. V. Landa (No. 12); *B. vernus* (Curt.), adult: Czechoslovakia, South Bohemia, Vydra riv., Turnerova chata, 17. viii. 1976 leg. V. Landa (No. 13); *Baetopus* sp., adult: Mongolia, Chövsgöl, Tesinj gol riv., 14. viii. 1967 leg. Z. Kaszab (No. 14); *Centroptilum luteolum* (Müll.), adult: Czechoslovakia, Central Bohemia, Radotínský brook, Cíkána, 10. vi. 1976 leg. Z. Pádr (No. 15); *Rhithrogena semicolorata* (Curtis), adult: Czechoslovakia, Central Slovakia, Solisková voda stream, Važec, 15. vii. 1973 leg. T. Soldán (No. 16); *Habroleptoides modesta* (Hagen), subimago: Czechoslovakia, South Bohemia, brook, Komárov, 21. iv. 1949 leg. V. Landa (No. 17); *Habrophlebia lauta* Etn. adult: Bulgaria, brook, Novo Paničarevo, 30. vi. 1978 leg. T. Soldán (No. 18); *Ephemerella (Ephemerella) ignita* (Poda), subimago: Czechoslovakia, South Bohemia, Lužnice riv., Tábor, 9. viii. 1975 leg. J. Vilimová (No. 19).

All the material studied is preserved in 75% alcohol and is deposited in collection of the Institute of Entomology, Czechoslovak Academy of Sciences, Praha. Legs, wings and genital segments of specimens dissected were transferred directly into Canada balsam with Cellosolve. Fresh material, when available (specimens No. 10, 11 and 18) was dissected in physiological saline, fixed with Bouin (Duboseque-Brasil modification) and embedded into Paraplast. Sections of thickness 4–6  $\mu\text{m}$  cut on a microtome (gonads) were stained with Mayer's haematoxylin-eosin.

Both control larvae of *Baetis rhodani* and larvae infected with parasitic worms were kept to the adult stage in normal aquarium at a temperature  $15 \pm 1^\circ\text{C}$  and 18 hours light day. Water was changed daily and occasionally aerated.

## RESULTS

### Morphological characteristics of gynandromorphs

The head of mayfly gynander is either male or female without the occurrence of the opposite sex characters, or male and female portions are bilaterally symmetrical. No case of mosaic-like distribution of characters has been reported so far. In the Baetidae male characters on head are usually conspicuously manifested by a normally developed turbinate eye. There is either left turbinate eye (Grandi, 1962; Berner, 1949; Landa 1949; specimens No. 2, 5, 7, 15 — this case seems to be more frequent) or right turbinate eye (Berner, 1949; Bugg, 1954) present. In gynanders of the family Leptophlebiidae there is also bilateral gynandromorphism in structure, colour and size of compound eyes (Daggy, 1944; specimens No. 17, 18). Of course, there are further differences in the arrangement of antennae, ocelli and in colour patterns of head apparent especially in the Baetidae (see detailed description by Landa, 1949). Rarely (specimens No. 5 — Figs. 1, 4) certain male structures (small, modified turbinate eye) occur on the female half of head. If the head shows bilateral gynandromorphism, the male and female portions are always clearly distinguishable, no head portion of unclear origin have been reported. The specimens with male head occur only in the Baetidae (males with ovaries — specimens No. 3, 4). This cases are probably extremely rare, no such individuals are mentioned in literature. On the contrary, specimens with solely female head were found in other families (Siphonuridae, Heptageniidae, Leptophlebiidae, Potamanthidae, and Ephemeridae). These specimens, of course, have typical female eyes (Spieth & Ide, 1939; Bengtsson, 1928; Grimeland, 1963; Berner, 1957; No. 16). Some authors report the eyes of these gynanders "somewhat larger", e. g. Spieth & Ide (1939) for *Stenonema terminatum*.

Apart from several exceptions, the thorax of mayfly gynanders is mostly bilaterally symmetrical (including legs and wings) in the specimens of the Baetidae or predominantly female in other families where the gynanders occur. The tendency to mosaic-like

distribution is not so pronounced than that in abdomen although there are some cases indicating or resembling mosaics (No. 16). Bilateral distribution of characters and colour patterns (borders between male and female portions mid dorsal and mid ventral lines) is the most frequent case. Male portion of thorax can be either on the right hand or on the left hand (Bugg, 1954; Berner, 1949; Landa, 1969; Spieth & Ide, 1939; specimens No. 2,5). Bilateral symmetry on thorax occurs only in specimens with bilateral symmetry on head. Thorax symmetry can be of the opposite type than that in head. Male half of thorax on the right hand and male half of head on the left hand occur in specimens No. 2 (cf. Landa, 1949). Thorax symmetry is always longitudinal. Entirely female thorax was found by Grandi (1966) in *Baetis* and Spieth & Ide (1939) in *Potamanthus*, and in our specimens No. 1, 17, 18, 19. Also Bengtsson (1928) and Grimeland (1963) report female thorax in *Ameletus* gynanders. Entirely male thorax was found by Spieth & Ide (1939) in *Stenonema* and in our specimens No. 7, 15 (also specimens No. 3, 4 — males with ovaries-belong here). As far as the thorax of gynanders is concerned, there are two cases worth of our attention. In specimen No. 16 (*Rhithrogena semicolorata* — Figs. 6-9) there are male prothorax and fore legs while meso and metathorax with wings and middle and hind legs are not distinguishable from those of normal female. Judging from the colour patterns, the only case of mosaic-like distribution of male and female characters is known in *Hexagenia* (Berner, 1957). Although there are rests of bilateral symmetry in distribution of spots on the ventral side of thorax and on legs, mixture of male and female patterns indicates colour mosaic.

The pregenital abdominal segments of gynanders show mosaic-like distribution of characters in most specimens studied (Landa, 1949; Berner, 1949, 1957; Spieth & Ide, 1939; specimens No. 2, 5, 7, 15). No case of symmetry in distribution of secondary sexual characters has been described. Mosaic-like distribution of these characters is apparent only in species having sexual dimorphism in colour patterns since there is no dimorphism in shape of abdominal segments. In many specimens there are areas of unclear origin showing transitory types of colour patterns between males and females (cf. Landa, 1949; No. 5 — Figs. 1—5). No case of gynander with predominantly male characters was described. Either female segments or segment portions are prevailing (Berner, 1949, 1957; No. 15, 18) or male and female portions are approximately equally presented (Landa, 1949; Bugg, 1954; No. 5). The border between male and female portions of abdomen are usually not constituted according to abdominal segments, one segment can consist of both male and female portions. Mosaic-like distribution of characters occurs currently in the Baetidae, rarely in the Leptophlebiidae (cf. Spieth & Ide, 1939) and the Ephemeridae (cf. Berner, 1957). Entirely female pregenital abdominal segments in gynanders are referred by Bengtsson (1928) and Grimeland (1963) in *Ameletus* and by Grandi (1966) in *Baetis*. We found these conditions in specimens No. 16 and 19. Entirely male pregenital segments were found by Spieth & Ide (1939) in *Potamanthus* and in our specimens No. 3, 4.

Gynanders of mayflies, with some exceptions, always possess at least reduced forceps and/or penis lobes. Contrary to pregenital ones, the genital and postgenital segments often show a tendency to bilatellar symmetry in arrangement of male and female characters. The following cases were observed as far as male external genitalia are concerned: (i) both gonopodes are normally developed (Landa, 1949; No. 15, 18), penis lobes present or absent; (ii) both gonopodes are present but reduced in length or in number of segments (Daggy, 1944; Bugg, 1954; No. 1, 3, 5, 16, 18, 19). Except for the Baetidae (penis absent), penis can be normally developed (Spieth & Ide,

Table 1. Gynandromorphs, intersexes and external genitalia teratology in Ephemeroptera

Species	No. and stage of specimens	Collected in	Reference	Remarks
<b>A. family Siphonuridae</b>				
1. <i>Amelatus inopinatus</i> Etn.				
	1 adult		Bengtsson (1928)	
2. <i>A. inopinatus</i> Etn.				
	1 adult	Norway	Grimeland (1963)	
<b>B. family Baetidae</b>				
1. <i>Baetis alpinus</i> (Pictet)				
	2 adults	Roumania	Codreanu & Codreanu (1938)	supernumerary forceps
2. <i>B. alpinus</i> (Pictet)				
	2 adults	Czechoslovakia	present study	(No. 1-2)
3. <i>B. fuscatus</i> (L.)				
	1 adult	Czechoslovakia	Landa (1949, 1969)	typical gynandromorph
4. <i>B. fuscatus</i> (L.)				
	4 adults	Czechoslovakia	present study	(No. 3-6)
5. <i>B. muticus</i> (L.)				
	1 adult, 1 larva	Czechoslovakia	present study	(No. 7-8)
6. <i>B. rhodani</i> (Pictet)				
	1 adult	Belgium	Lestage (1922)	intersex
7. <i>B. rhodani</i> (Pictet)				
	4 adults, 5 larvae, 1 subimago	Roumania	Codreanu & Codreanu (1931)	probably intersexes
8. <i>B. rhodani</i> (Pictet)				
	1 adult, 1 subimago	France	Degrange (1960)	intersexes
9. <i>B. rhodani</i> (Pictet)				
	3 adults, 35 larvae, 1 subimago	Czechoslovakia	present study	intersexes (No. 9-12)
10. <i>B. scambus</i> Etn.				
	1 adult	Finland	Tiensuu (1937)	intersex
11. <i>B. vernus</i> (Curt.)				
	1 subimago	Czechoslovakia	present study	supernumerary forceps
12. <i>B. vernus</i> (Curt.)				
	1 adult	Czechoslovakia	present study	intersex
13. <i>Baetis</i> sp. ( <i>fuscatus</i> ?)				
	1 subimago	Finland	Tiensuu (1937)	intersex
14. <i>Baetis</i> sp.				
	1 adult	Italy	Grandi (1966)	(No. 13)
15. <i>Baetoptus</i> sp.				
	1 adult	Mongolia	present study	

Table 1 (continued)

Species	No. and stage of specimens	Collected in	Reference	Remarks
10. <i>Centroptilum luteolum</i> (Müll.)	1 adult	England	Bagg (1954)	gynandromorph (No. 15)
<i>C. luteolum</i> (Müll.)	1 adult	Czechoslovakia	present study	
11. <i>Cloeon simile</i> (Ent.)	1 adult	Finland	Tiensuu (1937)	
12. <i>Heterocloeon curiosum</i> (McDunn.)	1 adult	USA	Berner (1949)	typical gynandromorph
13. <i>Pseudocloeon</i> sp.	1 adult	USA	Berner (1949)	
C. family Heptageniidae				
1. <i>Stenacron interpunctatum</i> (Say)	1 adult	USA	Needham, Traver & Hsu (1935)	gynandromorph (No. 16)
2. <i>Stenonema rubromaculatum</i> (Clemens)	1 adult	USA	Spieth & Ide (1939)	
3. <i>S. terminatum</i> (Walsh)	1 adult	USA	Spieth & Ide (1939)	
4. <i>Rhithrogena semicolorata</i> (Curt.)	1 adult	Czechoslovakia	present study	
D. family Leptophlebiidae				
1. <i>Hobropleptoides modesta</i> (Hag.)	1 subimago	Czechoslovakia	present study	gynandromorph (No. 17)
2. <i>Habroplebia lauta</i> (E.)	1 subimago	Bulgaria	present study	
3. <i>Leptophlebia cupida</i> (Say)	1 adult	USA	Daggy (1944)	gynandromorph (No. 18)
4. <i>L. nebulosa</i> (Say)	1 adult	USA	Daggy (1944)	
6. <i>Paraleptophlebia mollis</i> (E.)	1 adult	Canada	Spieth & Ide (1939)	
E. family Ephemerellidae				
1. <i>Ephemerella ignita</i> (Poda)	1 subimago	Czechoslovakia	present study	gynandromorph (No. 19)
F. family Ephemeridae				
1. <i>Hezagenia munda elegans</i> Traver	1 adult	USA	Berner (1957)	gynandromorph
G. family Potamanthiidae				
1. <i>Potamanthus verticis</i> (Say)	1 adult	USA	Spieth & Ide (1939)	

1939 — *Paraleptophlebia*; No. 19), reduced in size or completely absent (No. 16); (iii) bilateral symmetry occurs in male external genitalia: either left or right gonopode (reduced or normal) is present (Berner, 1949 — *Pseudocloeon*; Berner, 1957; Spieth & Ide, 1939 — *Stenonema*; No. 2, 4, 17). Penis (if present) is normally developed (Spieth & Ide, 1939) or one penis lobe is lacking (Berner, 1957) In the *Potamanthus* gynander only one penis lobe but both gonopodes are developed (Spieth & Ide, 1939). Reduced penis lobes in *Ameletus* gynander with forceps lacking are described by Grimeland (1963); (iv) all male external genitalia are lacking (Grandi, 1966; Berner, 1949 — *Heterocloeon*). Female external genitalia are either lacking or normally developed in gynanders with female pregenital segments (cf. Grimeland, 1963). We found reduced female openings also in specimens No. 3, 4 where pregenital segments were entirely male. Reduced openings (posterior margin of sternum VII not produced) were observed in specimens No. 16. Vestibulum was considerably reduced as well.

The postgenital segments (tergum X, paraprocti, epiproct and cerci with paracercus) always show bilateral symmetry (cf. Landa, 1949; No. 5) or they are entirely male (cf. Spieth & Ide, 1939; No. 3, 4) or entirely female (cf. Grandi, 1966. No. 16, 19).

### Gonads of gynandromorphs

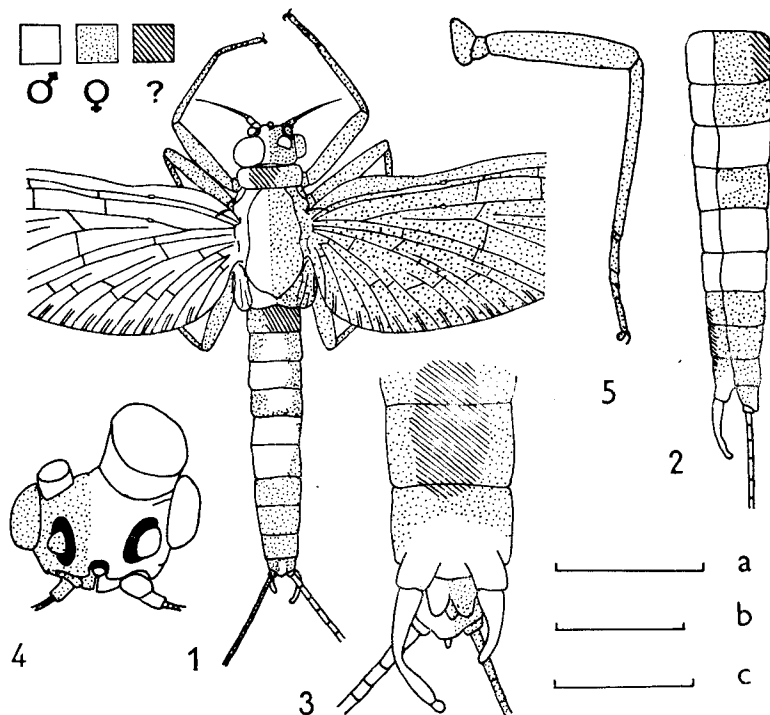
Since no true gynander was studied in the larval stage, gonads are described only in adults where testes are atrophied and empty and dilated oviducts are filled up with the eggs. In all specimens studied at least reduced gonads are present. As with the external characters, femal features prevail in internal organs as well — ovaries or their rests were found in most specimens. We found fully developed ovaries only in specimens No. 3 and 7. In remaining specimens with eggs in the abdominal cavity there were only reduced oviducts and reduced number of eggs present (No. 1, 4, 7, 16, 18, 19). However, previous oviposition cannot be excluded in specimens with normally developed openings. On the other hand, dilated oviduct usually reach only to abdominal segments II or III (No. 4, 7, 18) so that ovaries are apparently reduced. Also Spieth & Ide (1939), Berner (1949) and Grimeland (1963) found eggs in the abdominal cavity. In these specimens male ducts are sometimes present (No. 3, 4, 7, 16, 19) but they represent only ductus ejaculatorius and slight posterior portion of was deferens. Seminal vesicle and rests of testicular follicles were never found (cf. Landa, 1949). No spermatozoa were observed on sections (No. 7, 16). Similar conditions were found also in specimens without eggs in abdomen. Reduced seminal vesicles were observed in specimens No. 1 and 15 but their content could not be studied because of poor preservation.

Codreanu & Codreanu (1931) described larva with both functional testes nad ovaries: “.gonades formées de follicules produisant des spermatozoides en quantité massive et communiquant toutefois avec des oviductes typiques...”. Judging from external characters, this specimen might belong rather to intersexes, despite absence of parasites. We studied similar specimen of *Baetopus* (No. 14). Although the ovaries were normally developed and male ducts present we failed to find seminal vesicles and spermatozoa or rests of testicular follicles.

### Morphological characteristics of intersexes induced by mermithid parasitism

Contrary to gynanders, the individuals showing intersexual arrangement of somatic characters represent predominantly females with intermediately developed

male characters. As far as the intersexes are concerned, no case of symmetrical arrangement of characters was observed in our material. The occurrence of male characters is restricted to head and last abdominal segments (especially sternum IX). In typical intersexes, the thorax including wings and legs and abdominal segments I-VIII is always of the female character. The below description concerns intersexes induced by a mermithid parasitization.



Figs. 1-5: Gynandromorphism and intersexuality in the Ephemeroptera. Gynander of *Baetis fuscatus* (L.), specimen No. 5. 1 - whole specimen, dorsal view. 2 - abdomen, lateral view. 3 - last abdominal segments, ventral view. 4 - head, frontal view. 5 - fore leg. Scale A (Fig. 1): 2.5 mm. Scale B (Fig. 2): 3.4 mm. Scale C (Figs. 3-5): 1.7 mm.

Intersexual individuals usually possess a pair of turbinate eyes between normally developed female eyes. These turbinate eyes are by  $1/2-2/3$  smaller than normally developed ones in males. Although they are of the same colour as those in males, they are differently shaped, usually much more rounded. Light ring, present in some *Baetis* species is always lacking. In our material we found these conditions in most *Baetis* intersexes studied (specimens No. 6, 11, 12, 13). Male turbinate eyes of intersexes are usually of the same size (No. 13, 14) but sometimes one eye is larger than remaining one (No. 11). Also Codreanu & Codreanu (1931) and Tiensuu (1937) described similar cases. Development of one reduced turbinate eye is probably very rare; we found only three female larvae (No. 10) having the analgen of either only left (2 cases) or only right (1 case) male eye developed. Contrary to reduced male genitalia, which can be studied solely in adults, growing turbinate eyes are well visible under the cuticle of older larvae.

Intersexual individuals are characterized also by considerably modified forceps present on the posterior margin of abdominal sternum IX. Similarly to those of some gynanders, the forceps are often only one-segmented and much shorter than forceps of normal males (No. 11, 13). The same case is mentioned by Tiensuu (1937). In one specimen of our material (No. 6) the forceps are remarkably reduced and only forceps base resembles that of normal male.

#### Gonads of intersexes and infected specimens

As it has been mentioned above, the occurrence of intersexes in populations of some *Baetis* species is evidently connected with infection of larvae by larvae of parasitic worms from the family Mermithidae. In order to study the effects of parasitization on host gonads we dissected several hundreds of larvae of *Baetis rhodani* of which 163 larvae were parasited (mermithid larva present in body cavity of host larva). Of these, there were 151 female larvae (92.64%) and only 12 male larvae (7.36%).

The dissections of male larvae revealed that all the larvae were castrated (none of them with intersexual characters on head or abdomen). These larvae had died before the subimaginal moulting started. No rests of testes were found. Among 151 infected female larvae (the mortality in laboratory less than 10%), there were 35 larvae (23.2%) showing intersexual characters. These individuals exhibited full castration again. Histological treatment of last abdominal segments (VII-IX) enabled to recognize rests of oviducts not distinguishable during dissections. No ovaries were found in abdominal cavity of any larvae filled up with coiled mermithid larva. Rests of oviducts completely disappear in adults (No. 6, 11) so that castration caused by mermithid larvae in larval stage results in complete sterility of adults.

Infected larvae, which do not possess intersexual characters, represent various degrees of reduction of gonads. Some ovarioles and even those forming previtellarium were found in several specimens while in the others they are heavily damaged. In these cases germinal and follicular cells are indistinguishable, ovarioles are filled with degenerating tissues containing lysed oocytes with pycnotic nuclei and they do not form any egg chambers. In most specimens infected the vitellogenesis does not start at all, vitellarium as well as previtellarium are disintegrated before starting of yolk secretion.

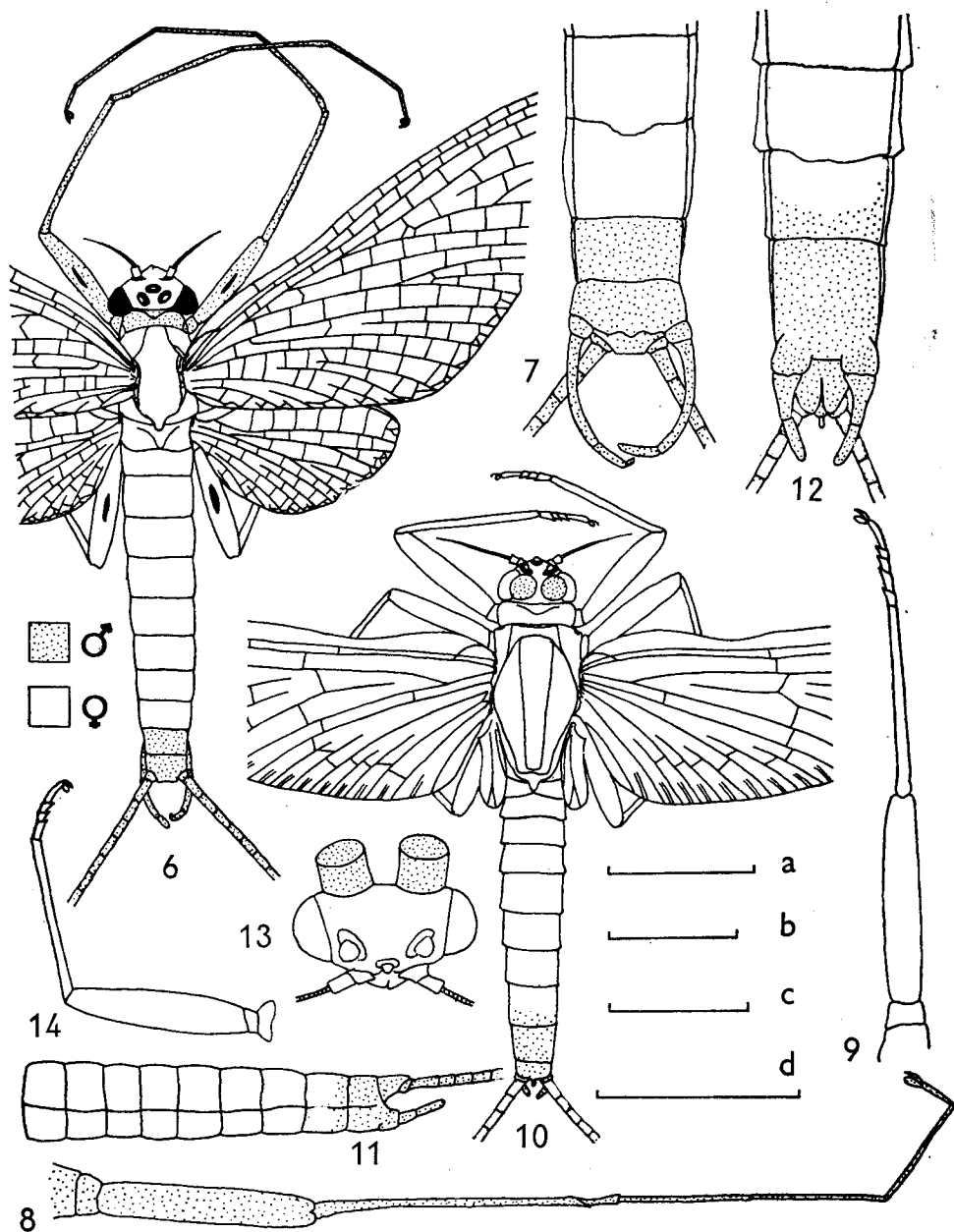
The ovarioles number cannot be usually stated because of resorption of ovary as a whole but it is undoubtedly strongly reduced. Some ovarioles of some specimens infected can probably give rise to several eggs, despite resorption of rest of ovary. The eggs are then present in abdominal segments of adult females without intersexual characters. In spite of the occurrence of some eggs, these individuals are practically sterile because the total fecundity is reduced to 0.5—1.0% in comparison with control females fecundity. In six adults, which have undergone mermithid infection in larval stage, 13, 29, 36, 41 and 68 eggs respectively were found.

After the mermithid larva leaves the body of host mayfly larva, the mortality of mayfly larvae will remarkably increase. We managed to rear to the subimaginal and imaginal stages only 14 larvae of which 4 were intersexes. Remaining larvae quickly died probably of a secondary infection.

#### Teratology of external genitalia

Apart from teratology of external male genitalia described in many specimens of gynanders and intersexes and discussed in respective paragraphs, there are some cases of atypical arrangement of forceps which are evidently not connected with atypical arrangement of secondary sexual characters. These cases are mentioned





Figs. 6–14: Gynandromorphism and intersexuality in the Ephemeroptera. Gynander of *Rhithrogena semicolorata* (Curt.), specimen No. 16 (Figs. 6, 7, 8, 9); intersex of *Baetis vernus* (Curt.), specimen No. 13 (Figs. 10, 11, 12, 13, 14). 6, 10 – whole specimen, dorsal view. 7, 12 – last abdominal segments, ventral view. 8, 14 – fore leg. 9 – hind leg. 11 – abdomen, lateral view. 13 – head, frontal view. Scale A (Fig. 6): 3.3 mm. Scale B (Figs. 7–9, 12–14) 1.6 mm. Scale C (Fig. 10) 2.5 mm. Scale D (Fig. 11) 3.0 mm.

in literature only in males, no cases are known as far as relatively less known female external genitalia are concerned. There are two distinct types of teratology in male external genitalia: supernumerary forceps and deformed forceps on the hind margin of sternum IX (in normal position).

Supernumerary forceps were observed posterolaterally on hind margin of abdominal sternum VIII which may be arranged similarly to tergum IX including a pair of sclerites near the basis of forceps. In addition to supernumerary forceps normal forceps on sternum IX are present. Codreanu & Codreanu (1938) describe two specimens of *Baetis alpinus* (Table I) having supernumerary forceps: there is either a pair of gonopodes or only right gonopode on sternum VIII. All supernumerary forceps are of the same length as normal ones and normally segmented. We observed a specimen of *Baetis vernus* (No. 12) having a reduced left gonopode on sternum VIII. This gonopode is by 1/2 shorter than the normal one on sternum IX and its basis is not modified at all.

We found several cases where deformed or reduced forceps were present in the genera *Baetis* and *Cloeon* (family Baetidae). Forceps are usually only one- or two-segmented and always differently shaped. Basal segment, which is characteristic in normal males, is never discernible in these individuals. Forceps reach only 1/3—2/3 of the normal length. In all the cases investigated the whole segments IX and X with paraprocts, epiproct and cerci are smaller and less sclerotized than in normal males. In all these cases both gonopodes, although of different shape, are present.

Teratology of male external genitalia has been observed only in the family Baetidae so far. That is why we have no data concerning the teratology of penis. The openings of ducts in cases studied are usually unaffected, openings are present only on the hind margin of segment IX (specimens No. 12). In specimens with deformed forceps the duct openings are only slightly modified (more membranous) and never interrupted. Gonads (testes) of specimens investigated were always normal.

#### Habits of gynandromorphs and intersexes

There are only several data concerning the habits of gynanders and intersexes during the emergence and mating flight. These specimens are mostly identified in fixed material so that the habits and nature of gynandromorphs and intersexes can be only indirectly deduced.

The typical gynander of *Heterocloeon curiosus* described by Berner (1949) was collected in the female swarming (about 50 specimens collected) from 1.45—3.30 p. m. where no males were present. Females flew over the swiftest part of the river occasionally dropping down to the water. The second gynander described by Berner (1949) was caught together with males and females but at the time of collecting the specimens were not flying in swarms but individually with males rising and falling in the manner typical for the Baetidae.

The specimens No. 5 and 18 were behaving as males when collected. They were present in male swarms containing about 1000 (No. 5) and 100 (No. 18) males respectively. Also the gynandromorph of *Rhithrogena semicolorata* (No. 16) was collected together with about 50 males in swarm which was individually entered by unfertilized females. Landa (1949) reports his specimens behaving as males as well. On the other hand the gynander of *Centroptilum luteolum* (No. 15) was caught together with about 10 females during the compensatory flight before oviposition.

Masculinized females, which have undergone a mermithid parasitism, were always behaving as typical females when collected. They were usually caught in the female swarm (No. 13 and others). Completely sterile intersexes are present in female

swarms as well (e. g. No. 11). The intersex of *Baetis fuscatus* (No. 6) was found even ovipositing on submerged stones together with normal females. With the exception of higher sensitivity of the latter to temperature and oxygen content no differences between habits of normal and masculinized larvae of *Baetis rhodani* (No. 10) were observed. Infected larvae mostly do not molt and exhibit much higher mortality than those in controls. Specimens showing teratology in male external genitalia always behave as typical males.

#### DISCUSSION

As it is apparent from the above paragraphs, there are three distinct categories of deviations in the arrangement of secondary sexual characters and copulatory organs in the Ephemeroptera. However, the distinction between these individual categories (gynanders, intersexes, external genitalia teratology) seems to be rather arbitrary. In classifying our material we followed these principles: (a) specimens with both male and female parts of body mostly normally developed were considered as gynanders; (b) specimens showing predominantly female characters with fundaments of turbinate eyes and reduced forceps, and especially those where previous parasitism could be detected, were considered as intersexes — masculinized females; (c) specimens with only male (female) somatic characters normally developed and copulatory organs differently developed were called “teratology of external genitalia”. Although there are undoubtedly some difficulties in applying these principles, e. g. apparent gynanders sometimes possess “intersexually” developed characters or reduced forceps, this classification enables to separate true intersexes and gynanders. Agnew (1979) believes that genetically conditioned intersexuality does not exist and that “sometimes the gynanders have been erroneously referred to as ‘intersexes’”. If such cases do exist within the Ephemeroptera, they are indistinguishable from gynanders having some characters intermediately developed. On the other hand, masculinization of *Baetis* females caused by parasitism represents true intersexuality and at least this type of intersexuality is proved in mayflies. Some earlier authors regarded also these individuals incorrectly as “gynandromorphs” (cf. Agnew, 1979).

As it is obvious from Tables I and II, both quantitative and qualitative presentation of gynanders, intersexes and external genitalia teratology are irregular within the mayfly families. If these phenomena are analyzed, we can find several remarkable aspects:

(i) The occurrence of gynanders and intersexes is restricted only to Europe and North America with the exception of one specimen (No. 14) from Mongolia. This phenomenon can be simply explained by the fact that detailed treatments of mayfly fauna have been made only in these Holarctic regions. Faunistic study is always connected with sampling of great numbers of specimens where the probability of gynandromorphism or intersexuality detection is much higher. Apart from some individual findings, gynanders were always caught among several hundreds of specimens (cf. Berner, 1949, 1957; Landa, 1949, and others). We found the specimens No. 5, 16, 18 among numerous normal individuals in swarms as well. There is no doubt that gynandromorphism is not restricted geographically and further specimens will be found also in the remaining biogeographical regions. However, the occurrence of intersexes depends on the distribution of parasites causing masculinization of infected females (worms from the family Mermithidae).

(ii) Gynanders are numerous in families containing a large number of species (see Table II). There is direct correlation between the number of known gynanders

Table 2. Occurrence of gynandromorphs, intersexes, and external genitalia teratology within the families

Family	No. of species reported		No. of specim. reported (adults only)		Total No. species in Europe and North America <sup>+</sup>	Degree of sexual dimorphism
	No.	%	No.	%		
A. Siphonuridae	1	3.8	2	4.3	12 + 81	+
B. Baetidae	13	50.0	33	70.2	56 + 128	+++
C. Heptageniidae	4	15.5	4	8.5	76 + 152	+
D. Leptophlebiidae	5	19.3	5	10.7	25 + 70	++
E. Ephemerellidae	1	3.8	1	2.1	10 + 85	++
F. Ephemeridae	1	3.8	1	2.1	6 + 13	+
G. Potamanthidae	1	3.8	1	2.1	1 + 8	+
<b>Total</b>	<b>26</b>	<b>100</b>	<b>47</b>	<b>100</b>	<b>186 + 537</b>	

<sup>+</sup> calculated from Puthz (1978) and Edmunds (1978)

and the number of species included. The most numerous mayfly families — Baetidae, Heptageniidae and Leptophlebiidae — comprise more than 80% of known gynanders and 100% of intersexes while the occurrence of gynanders in families with smaller number of species (e. g. Ephemeridae and Potamanthidae) is very low. On the other hand, only three cases of gynandromorphism were detected in relatively numerous families Ephemerellidae and Simphonuridae. This phenomenon is probably due to the fact that species from numerous families are more frequently collected and by a higher probability of spontaneous gynandromorphism in these families. The same reasons cause the higher occurrence in widespread and abundant species. Species of the genus *Baetis* comprising most of gynanders studied belong to the most common species in Europe and North America.

(iii) Gynanders are mostly detected in mayfly groups with high degree of sexual dimorphism and nearly unknown in groups with sexual dimorphism only slightly developed. There is again direct correlation between occurrence of gynanders and degree of sexual dimorphism (see Table II). The highest degree of sexual dimorphism (turbinate eyes, legs, wings, colour patterns, cerci) occurs in the Baetidae (most of known gynanders), only slight dimorphism occurs in Ephemeridae and Potamanthidae (only two cases of gynandromorphism). The high degree of sexual dimorphism undoubtedly enables easy detection of gynanders and intersexes while in other families they can easily escape our attention. In the *Hexagenia* gynander described by Berner (1957) male and female body parts were distinguished only according to colour patterns, there were no somatic characters distinguishing males and females.

According to literary data and in our material we found three principal types of gynanders: bilateral gynanders, predominantly females and predominantly males. Bilateral gynandromorphism is apparent solely on head and thorax (cf. Berner, 1949; Landa, 1949; Bugg, 1954; Grandi, 1966), abdomen of these specimens always shows mosaic-like distribution of males and females characters. Gynanders with predominantly female characters usually possess male eyes and some of male terminalia (cf. Spieth & Ide, 1939; Daggy, 1944). Gynanders with predominantly male characters are described for the first time (No. 3, 4). There are only slightly modified external genitalia and eggs present in abdomen, no further female characters occur. As it noted by Agnew (1979) there are two remarkable points within the mayfly gynanders: male parts sometimes occur on both sides of symmetry and some body areas (e. g. colour patterns on abdomen) are atypical, neither female nor male.

Gonads of gynanders are always either male or female but both testes and ovaries are usually reduced in size and in ovarioles (eggs) number.

Although mayfly gynanders are known for more than 50 years and the origin of gynanders in general became explained at the beginning of this century in *Drosophila*, no attempts to explain this phenomenon in the Ephemeroptera have been made. Only Grimeland (1963) reports that it is caused by „disturbance of the XX-XY mechanism”. At present, when basic data concerning sex determination in the Ephemeroptera have been published (Katayama, 1939; Kiauta & Mol, 1977; Mol, 1978) the interpretation of mayfly gynandromorphism is presented by Agnew (1979): “Gynanders arise from XX female zygotes with early loss of an X in one cell line giving rise to subsequent male tissues (XO karyotype); there appears to be some mixing (more so than in *Drosophila*) of cleavage nuclei during the syncytial divisions because of the islands. While sex per se (as seen in gonads and secondary sex characters such as eyes, legs and genitalia) is autonomous, pigmentary phenotype is less so, probably because of diffusible substrates or products”. This explanation, although involving account for anomalous colour patterns, cannot be applied for species where another type of sex determination occurs (XX ♀♀/XY ♂♂, e. g. in *Ecdyonurus* or *Ephemerella* (cf. Mol, 1978). We believe that also further interpretation of gynandromorphism in mayflies might be used. Spontaneous frequency of mayfly gynanders seems to be relatively very high in comparison with that of other insects (1.2–3.0 in  $10^4$  in *Drosophila*). In some mayfly families this frequency is higher by at least an order than in *Drosophila*. The relatively higher frequency of gynanders in Ephemeroptera may be due to parthenogenesis and polyspermy. Gynanders of this origin have been experimentally evoked in some other insect orders. After starting parthenogenetic embryogenesis (cleavage) some nuclei can be fertilized anyway and can give rise to subsequent male tissues. The probability of fertilization of these nuclei is increased by poly- or dispermy. Presence of males in parthenogenetic population is necessary. With the exception of polyspermy, which has been discovered only in the genus *Baetis* so far (Bohle, 1969) all these phenomena (parthenogenesis, occurrence of males in parthenogenetic populations) are widespread within the Ephemeroptera. Diploid thelytoky was described in nearly 100 species (Degrange, 1960; Needham et al., 1935 and others), tytoparthenogenesis is present probably in all species. Males are often found in apparently parthenogenetic populations (Needham et al., 1935; Landa, 1969). Moreover, diploidy in parthenogenetic eggs is reached probably after oviposition.

In comparison with causes of gynandromorphism, causes of intersexuality are more evident. Masculinized females have been found only in the genus *Baetis*, in individuals infected with worms from the family Mermithidae (Nematoda, Enoplida). Parasited larvae of several *Baetis* species are currently found (Murphy, 1922; Degrange, 1960; Benech, 1972; Sukop, 1973) but only some specimens (10–40 are masculinized and may give rise to intersexual adults. Although mermithids were found in other genera (e. g. *Callibaetis* — Peters & Arvy, 1979) of Baetidae and in other families (e. g. Heptageniidae — Muttkowski, 1929; Caenidae — Arvy & Peters, 1979) no cases of intersexuality have been reported. Rubtsov (1977) reports further 8 families of aquatic nematods parasiting in the mayfly larvae but masculinization of mayflies and other aquatic insects (aquatic Diptera and Heteroptera) is caused only by species of the family Mermithidae.

Contrary to gynanders, development of male secondary sexual organs is restricted only to turbinate eyes and external genitalia forceps. Although the masculinization of larvae is relatively abundant in infected population, the quantitative representation

of these intersexes in adults is low because of high larval mortality. Our results concerning the mortality of infected male larvae (100%) fully agree with those obtained by Degrange (1960). He believes that male larvae do not represent a sufficient food supply for the parasite larva so that the larva of mermithid destroys also remaining necessary organs (gut, central nervous system) which results in the death of the host larva. The same might be applied in the case of infection of younger larvae. Older female larvae are able to provide mermithid parasite with sufficient amount of food (developed ovaries and large fat body are resorped). This explanation could be accepted in the case of mayflies only. In other insects, e. g. in Homoptera-Delphacidae, feminization of males was described after mermithid parasitization. Although no data concerning changes in neurosecretory organs of specimens infected are available, the hormonal interaction between host and parasite and damage of host CA and neurosecretory cells in brain can be supposed. Moreover, there are considerable irregularities in moulting cycles or their suppression in host larvae infected. On the other hand, selective mortality, which is sexually determined, cannot be explained by this way (sexual hormones are not present in insects and their absence is supposed to be evidenced just by the existence of gynanders and intersexes). The adult intersexes, apart from complete or nearly complete sterility are always behaving as typical females. Otherwise the behaviour of gynanders does not probably depend on morphologically prevailing secondary sexual characters. Destruction of gonads of intersexes and infected mayfly larvae shows typical characters of developing progressive sterility. Contrary to gynanders, gonads are gradually resorped and histological changes of both germinal and follicular cells can be compared with those caused by radiation or chemosterilization (diffusing of nuclei and oocyte ooplasm, pycnoses, break-down of follicular epithelium etc.). Contrary to some other insects infected with larvae of mermithids, infected mayfly females are nearly always sterile, only exceptionally several eggs are developed. In some other insects (e. g. bark-beetles) the fecundity of females is only slightly reduced or unaffected.

As far as the teratology of external genitalia is concerned, there are two distinct types of teratology in male copulatory organs; in females no cases have been described so far. The occurrence of supernumerary forceps is undoubtedly caused in embryogenesis and probably conditioned genetically (different segmentation of last abdominal segments and their appendages). Supernumerary forceps can be either normal in shape and length (Codreanu & Codreanu, 1938) or smaller and deformed (specimen No. 12). On the other hand, deformed forceps in normal position are most probably due to a regeneration of lost appendages and respective segments during larval development. Similar shape deformations can be observed on regenerated legs, gills and mouthparts. Oppenheim (1908) and Schmidt (1955) found that regeneration of abdominal segment X or segments IX and X with respective appendages was usual after experimental amputation in *Cloeon dipterum*. Apart from appendages and pseudocuticle, respective internal organs (tracheae, alimentary canal and probably also terminal portion of vas deferens and vas efferens) are regenerated. This regeneration occurs in other genera of the family Baetidae and in other genera as well.

As it is apparent from the foregoing paragraphs, the study of gynandromorphism, intersexuality and external genitalia teratology in the Ephemeroptera can elucidate not only special but also some general problems. Especially genetic analyses of wild specimens, attempts of experimental induction of gynanders in connection with parthenogenesis and hormonal interactions host-parasite in intersexes are worth of our attention.

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