Enicocephalomorphan and dipsocoromorphan fauna of W. Palaearctic (Heteroptera): composition, distribution and biology

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ABSTRACT The suborders Enicocephalomorpha and Dipsocoromorpha are the earliest extant offshoots of Heteroptera. Both groups are essentially pantropical and panaustralian, and in the Holarctic they occur mainly along its S fringe. Taxonomy and distribution of W Palaearctic species is imperfectly known; hence the present review is focused at general biology, and generic composition and affinities.

Enicocephalomorpha: (1) Enicocephalidae. Occuring only along the S fringe, the few finds are accidental or made during aerial dispersal/mating activity. All species of the arid zone are probably semiedaphic litter dwellers. *Systelloderes* (pangeic): Middle East only; all species belong to *S. occulatus* group and will be classified in new, endemic genera. *Henschiella* (panoriental, i.e. Afrotropical, Madagascan, Oriental, Papuan, Australian). *Oncylocotis* (panoriental). *Vuorilinna*: endemic to Saudi Arabia (related to Afrotropical-Madagascan *Embolorrhinus*).

Dipsocoromorpha: (2) Ceratocombidae. *Ceratocombus* (pangeic, probably paraphyletic): all over W Palaearctic (southern species unrecorded and undescribed); interstitial, in humid litter, northern *C. corticalis* in decaying wood. (3) Dipsocoridae. *Cryptostemma* (pangeic): all over W Palaearctic; interstitial, in gravel along clean streams; subamphibious, turning to plastron respiration when flooded. *Pachycoleus* (Palaearctic and Neotropical): in W Palaearctic mainly in north; interstitial, in wet mosses in swamps and along stagnant water bodies. (4) Schizopteridae. *Pinochius* (Afrotropical): accidental find of one species in Egypt; tropical species interstitial in forest litter.

IZVLEČEK FAVNA SKUPIN ENICOCEPHALOMORPHA IN DIPSOCOROMORPHA (HETEROPTERA) ZAHODNEGA PALEARKTIKA: SESTAVA, RAZŠIRJENOST IN BIOLOGIJA Podreda Enicocephalomorpha in Dipsocoromorpha sta filogenetsko najzgodnejši danes živeči skupini stenic. Obe skupini sta v bistvu pantropski in panaustralski, v holarktiku pa živita predvsem vzdolž njegove južne meje. Taksonomija in razširjenost zahodno palearktičnih vrst sta slabo poznani; zato ta pregled podaja predvsem splošno biologijo teh stenic, sestavo rodov in njihovo sorodnost.

Enicocephalomorpha: (1) Enicocephalidae nastopajo samo ob južni meji areala, maloštevilne najdbe so priložnostne ali pa so v zvezi z njihovo selitvijo in rojenjem. Vse vrste suhih predelov so verjetno semiedafske in živijo med organskimi ostanki. Rod *Systelloderes* je pangejski, v zahodnem palearktiku živi le na Bližnjem vzhodu. Vse vrste spadajo v skupino *S. oculatus* in bodo uvrščene v nove endemične rodove. *Henschiella* (panorientalski, t.j. afrotropski, madagaskarski, orientalski, papuanski in avstralski rod); *Oncylocotis* (panorientalski); *Vuorillina*: endemičen rod v Saudski Arabiji (soroden z afrotropsko-madagaskarskim rodom *Embolorrhinus*).

Dipsocoromorpha: (2) Ceratocombidae. *Ceratocombus* (pangejski, verjetno parafiletski rod): nastopa po vsem zahodnem palearktiku (južne vrste so še neznane in neopisane). Nastopa v vlažnem organskem drobirju, severna vrsta *C. corticalis* v razpadajočem lesu. (3) Dipsocoridae. Rod *Cryptostemma* je pangejski: nastopa po vsem zahodnem palearktiku. Živi med peskom in prodom vzdolž čistih tekočih voda. Je subamfibijski, ob poplavah preide na plastronsko dihanje. Rod *Pachycoleus* je palearktičen in neotropski: v zah. palearktiku živi predvsem na severu, v vlažnem mahu v močvirjih in ob stoječih vodah. (4) Schizopteridae - rod *Pinochius* je afrotropski: znana je le slučajna najdba iz Egipta. Vrste tega rodu živijo intersticijalno v gozdnem organskem drobirju.

According to the cladogenetic hypotheses and phylogenetic classification of ŠTYS (1984a, b, 1985, 1989) and SCHUH (1986), also supported by Cobben's and Andersen's investigations, the Enicocephalomorpha is a sister-group of all the other true bugs, the Euheteroptera, and, in turn, the Dipsocoromorpha is a sister- group of the rest of euheteropterans, the Neoheteroptera. Hence the general interest in all aspects of systematics and biology of these bugs.

Here I present an overview of the taxonomy, distribution, affinities and biology of a poor and little known fauna of the Western Palaearctic (only for convenience understood as covering Europe, the Mediterranean and Middle East, including the whole Arabian peninsula). The overview is partly based on unpublished data; its aim is to consider the scattered data on W Palaearctic fauna in a global context, to provide an impetus for collectors in the Mediterranean area to search for the taxa concerned, and to investigate in the field the relevant aspects of their biology. A full coverage of the literature is not intended.

1. Enicocephalomorpha

The Enicocephalomorpha include now (ŠTYS 1989) two families, the Enicocephalidae with 5 subfamilies and the Aenictopecheidae with 4. Only the species of the nominotypical subfamily Enicocephalinae occur in the area, and only in its arid southern fringe. The distribution of the subfamily is pantropical and panaustralian, some species penetrating into regions of temperate climate in the Nearctic, Tibet, Himalayas and Japan. There are only scattered records from the W Palaearctic, and the fauna is undoubtedly richer than we know. For instance, with the exeption of a single specimen from Aswan, no record of enicocephalids is available from N Africa.

1.1. Taxonomy and distribution

The Palaearctic fauna has been reviewed by ŠTYS (1970b), but some new records are available. The family contains the following genera occuring in the area:

(1) The monotypic genus *Vuorilinna* Štys with *V. carayoni* Štys from Saudi Arabia; it is a sister-genus to *Embolorrhinus* Jeannel that is distributed in Afrotropical and Madagascan regions.

(2) *Oncylocotis* Stal is a species-rich Panoriental genus ("Panoriental" meaning distributed all over the Eastern Hemisphere, including the southern fringe of the Palaearctic but excluding New Zealand) containing a high number of undescribed species. *Oncylocotis occipitalis* (Jeannel) was recorded from Aswan in Egypt; the specimen seems to be lost, and its subspecific assignment is unknown. The species is Afrotropical, with nominotypical subspecies occuring in the northern, and *O. occipitalis meridionalis* Štys in the southern part of the region. The other species is *O. basalis* subsp. n. (?) occuring in Yemen (unpublished); the species is widely distributed, with *O. basalis basalis* (Westwood) living in the Oriental, and *O. basalis curculio* (Karsch) in the Afrotropical region.

(3) *Henschiella* Horváth is also a Panoriental genus, and *H. pellucida* (Horváth) has been recorded (ŠTYS 1968) from Yugoslavia, Turkey (Anatolia), Armenia, Uzbekistan and Turkmenia. The original finding of a single specimen in the town Bileća in Hercegovina, Yugoslavia (HORVÁTH, 1888) is so far the only record of the family from the European continent. An undescribed species (ŠTYS, in prep.) of *Henschiella* occurs in Israel.

(4) *Systelloderes* Blanchard is the only pangeic genus of *Enicocephalomorpha*, with many described species and a large number of undescribed ones. All Western Palaearctic species belong to the *S. uvarovi*-group as defined by ŠTYS (1970a); it includes 3 Palaearctic species (*S. uvarovi* Štys and *S. utukhengai* Linnavouri from Iraq, and *S. iranicus* Štys from Iran) and only one extralimital species *S. oculatus* Štys from Nigeria. All species of the *uvarovi*-group were based on single specimens. *Systelloderes* is probably a paraphyletic or polyphyletic genus delimited mostly by reductional characters, and the species of the *uvarovi*-group are characterized by striking plesimorphies in the construction of their male genitalia. New genera (possibly unrelated to *Systelloderes*) will have to be established for these species or species-aggregates. The problem will be tackled only after extensive new material from Iran, collected by the expedition of the National Museum in Prague and containing several species, will be studied.

1.2. Biology

Virtually nothing is known about the biology of W Palaearctic species. The family includes generalized predators, living essentially in interstitial spaces or crevices in soil or, if humidity is high enough, in litter, decaying wood, and other kinds of epigeic microbiotopes. All species or morphs capable of flight are attracted to light, form unisexual or bisexual mating swarms, and in the arid areas their flying activity usually starts exactly at

the onset of dusk. Nobody knows how the species living in arid areas penetrate deep in the soil and what exactly is their microhabitat. It has been the experience of all the hemipterists who have had a chance to collect enicocephalids in the Western Palaearctic or the transitional Saharo-Sindhian belt (Hoberlandt, Linnavouri, Remane, Štys) that even in biotopes where catches at light were rich, all attempts at finding the bugs in their natural environment failed *. The experience of American hemipterists is similar as summarized by Wygodzinsky and Schmidt in their monograph about to be published on American enicocephalids.

I assume that the enicocephalids in arid zones must live very deep in soil crevices and (or) cracks in dried mud, and that during warm season adults leave this habitat at dusk and during the night for their dispersal and nuptial flight. Actually, all the finds of enicocephalids in the Western Palaearctic were either accidental isolated adults found in epigeic habitats - or made during their flight: at lamp or by a net attached to a car, always at dusk or at night. Actual swarms were not observed in the area. The natural microhabitat of any of the W Palaearctic species is unknown, and no biotope preference can be deduced from the available data. There are unlimited oportunities of making basic biological observations for persons who happen to be at the right place at the right time. The swarms were not observed in the area, although swarming undoubtedly takes place. Many enicocephalid species have flightless females (and many have apterous, pterygodimorphic or pterygopolymorphic females or both sexes); the inability to fly may be characteristic of females of some species of the *Systelloderes uvarovi*-group.

2. Dipsocoromorpha

The dipsocoromorphans include predaceous, small-sized to miniature species (the smallest bug, a schizopterid species from Paraguay, about 0,5 mm long, is about to be described) living in various kinds or epigeic, semiedaphic and edaphic habitats providing an abundance of narrow interstitial spaces shared mainly with mites, symphylans, entognathan hexapods, and many other small-sized insects. Five families are presently

I recall my frustrating attempts to find the natural microbiotope of an unrelated but also relic and primitive group, the pentatomoid family Thaumastellidae in the Sudan; though the adults in the semidesert and Nile valley biotopes were abundant in light traps and other catches at light they actually flew to my bed when I was reading at night - I have never found a single specimen in its natural habitat. Also *Pachynomus* larvae were never found (and this applies to the pachynomids globally - J. CARAYON, pers. comm. to J. ZRZAVY).

recognized (ŠTYS 1970c, 1983, 1989): Schizopteridae, Ceratocombidae, Dipsocoridae, Stemmocryptidae and Hypsipterygidae; the former three occuring also in the W Palaearctic.

2.1. Schizopteridae

Schizopteridae (the suprageneric classification is not settled) is essentially a pantropical and panaustralian family, abundant in tropical forest floor litter which is its major habitat, with a score of undescribed genera and literally hundreds of undescribed species available in samples obtained by berlesating the litter and mosses or represented by flying morphs attracted to light. Its area extends in the N Hemisphere up to the State of Washington in the West, and up to Himalayas and Japan in the East. Only one W Palaearctic species, *Pinochius nitidicollis* Linnavouri from Egypt, is known. Its single recorded specimen was accidentally collected (Linnavouri, pers. comm.) in a hotel room in Giza. The other species of *Pinochius* Carayon live in forest litter in the Afrotropical region. I suspect that a more diversified fauna of schizopterids occurs in humid microbiotopes even in arid parts of the southern fringe of the West Palaearctic Schizopterid specimens could be discovered by berlesating the litter and carefully examining samples of the tiniest insects attracted to light.

2.2. Ceratocombidae

The next two families, Ceratocombidae and Dipsocoridae, are little diversified in the Western Palaearctic, but in suitable biotopes their individuals are often abundant. The general opinion about their rarity is unsubstantiated, but many heteropterists have never encountered them in the field simply because of not knowing their habitats.

2.2.1. Taxonomy and distribution

Ceratocombidae is a truly cosmopolitan family (for suprageneric classification see ŠTYS, 1982) including only 7 genera, and in W Palaearctic it is represented by several species of two subgenera of the genus *Ceratocombus* Signoret. *Ceratocombus* is a pangeic genus (occuring abundantly even in New Zealand; ŠTYS, in prep.) with numerous, largely

An interesting parallel to the isolated find of a representative of an essentially tropical and hygrophilous family in an arid zone is the recent discovery of a new genus and species of the tropical aquatic family Helotrephidae in arid areas of Afghanistan and Iran by PAPÁČEK, ŠTYS and TONNER (1989).

undescribed species living particularly in the tropics; some species extend far north (America: Canada, British Columbia sp. indet., ŠTYS in prep.; Europe: Kola peninsula).

The taxonomy of W Palaearctic species needs a thorough revision, and it is complicated by continuous pterygopolymorphism often affecting differently the local populations, and by a lack of knowledge of species-specific diagnostic characters of females. *Ceratocombus (Ceratocombus) coleoptratus* Zetterstedt is known from almost all of Europe, Siberia, Mongolia and the Far East. The second species, *Ceratocombus (Xylonannus) corticalis* Reuter is boreal, known from Finland, Poland, N Russia and the Far East, but I have recently found larvae which are probably of this species in the Eastern Carpathians in Czechoslovakia. The taxonomy and nomenklature of a third species, also belonging to the subgenus *Xylonannus* Reuter, is uncertain. According to KERZHNER (1974), there is only one species distributed in N and C Europe, and Central Asia. KERZHNER calls it *Ceratocombus (Xylonannus) brevipennis* Poppius (originally described from Kirghizia) and treats *C. lusaticus* Jordan, *C. jordani* Linnavouri (both from GDR) and *C. kunsti* Štys (from Czechoslovakia) as its junior synonyms. The synonymy is difficult to prove (or disprove) since the nominal species were based on different wing-morphs and sexes, but I suspect that at least two species of *Ceratocombus (Xylonannus)* other than *C. (X.) corticalis* - occur in C Europe. The problem will be dealt with in the near future, and to avoid any nomenclatural confusion by my tentative opinion, I shall call these species *Ceratocombus* sp. A and sp. B.

We have probably more unrecognized *Ceratocombus* species in the area, and I have seen odd specimens, unfortunately all of them of brachypterous females, also from northwestern Africa, the Canary Islands, and the Middle East (Lebanon, Syria).

2.2.2. Biology

Ceratocombus corticalis lives in decaying coniferous wood (I found larvae in the wood of *Abies*) in primeval northern and mountain forests.

Ceratocombus sp. A is a minute, usually a markedly brachypterous species living in extremely wet mats of *Sphagnum* in bogs together with *Pachycoleus*, *Chartoscirta* spp. and *Hebrus ruficeps*. Its population density is low so that the berlesating of *Sphagnum* is uneconomical, and it can best be collected by shaking out the *Sphagnum* over a sheet; not by sieving which usually destroys the fragile specimens.

The two common species, *Ceratocombus* sp. B and *C. coleoptratus* occur in many kinds of hygrophilous to subxerophilous biotopes, particularly in

* Bogs = "Hochmooren", fens = "Tiefmooren" in German.

sparse woods where the ground is covered by a deep and loose layer of sufficiently humid vegetable litter and (or) mosses providing many interstitial spaces. In an open country (moors, heaths) the population density of both species (which occur jointly) is low, and the specimens can be collected only individually and more or less accidentally. However, I have identified in Czechoslovakia three biotopes where both species are common and can be collected only abundantly by berlesating; one sample may yield hundreds of larvae and dozens of adults. Before taking samples it is advisable to ascertain the presence of *Ceratocombus* on the spot by individual searching.

The major biotopes are as follows: (1) Mesophilous to almost xerophilous *Pinus* or *Picea* woods with high and loose layers of needle litter mixed with herbaceous debris, typically in growths of *Pteridium aquilinum*. *Drymus* and *Stygnocoris* species occur in the same biotope. (b) Not too wet litter of reed and similar grasses on banks of stagnant water bodies; the associated heteropterans are *Scolopostethus pilosus*, sometimes *S. thomsoni* if *Urtica* is present, and *Saldula* and *Chartoscirta* species. The necessary condition is that under large pieces of reed debris there must be a deep and rottening layer of vegetable material with many interstices. Of the coleopterans, *Notoxus* species and many helodids and carabids are abundant in this biotope. (c) A still more preferred biotope is a sparse *Pinus-Betula-Alnus(-Quercus)* wood, especially at the fringes of lowland fens, with an undergrowth of *Vaccinium* species, grasses and sedges, and with the ground covered by mosses and moderately dry, yellowing *Sphagnum* (often penetrated by loose *Myrmica* nests). Both *Ceratocombus* species occur there along with *Drymus brunneus* and *ryeii*, *Eremocoris* larvae, and larvae and females of *Myrmedobia exilis*. This biotope may be moderately flooded after the spring thaw. Preliminary analysis of my samples suggests that both species are probably monovoltine and that the eggs hibernate.

Ceratocombus species in the tropics can be collected either by berlesating, or with a lamp or in pitfall traps. I have not yet tried to light-trap our species (moth individuals are flightless anyway), and so far no specimens appeared in pitfall traps laid by my colleagues studying spiders and carabids in suitable biotopes. However, *Ceratocombus coleoptratus* is often found in pitfall traps in the biotope (c) in the Netherlands (B. AUKEMA, pers. comm.).

2.3. Dipsocoridae

Dipsocoridae (= Cryptostemmatidae) is also a nearly pangeic family, but it is so far unknown from New Zealand, possibly only because no attention has been paid to the proper biotopes. The habitat preferences are globally uniform: the family had been unknown in Australia, but after my

suggestion as to where to search, HILL (1987) discovered and described the first few Australian *Cryptostemma* species, exactly in situations where I would look for them back home.

2.3.1. Taxonomy and distribution

The family includes only two genera, both represented in the W Palaearctic. *Cryptostemma* Herrich-Schaeffer is a nearly cosmopolitan genus, and owing to the monograph by JOSIFOV (1967) we know now 7 species from the area. Of the nominotypical subgenus, *C. alienum* Herrich-Schaeffer occurs all over (?) Europe and in the Caucasus, *C. carpaticum* Josifov in Poland and eastern Czechoslovakia (new record), *C. medium* Rey and *C. roubali* Josifov in the south of France, and *C. remanei* Josifov in Bulgaria and Italy (I may have missed some country records); of the subgenus *Harpago* Linnavouri *C. maroccana* E. Wagner from Morocco and *C. castaneovitreum* Linnavouri from Turkey (Anatolia) are known. Undoubtedly, other new species will be discovered in the Mediterranean and Middle East where suitable biotopes are common. I have seen odd specimens surely belonging to undescribed species from various parts of NW Africa, unfortunately all of them females, while the reliable diagnostic characters are mainly on the male abdomen and terminalia.

The other genus is *Pachycoleus* Fieber, often regarded as a subgenus of *Cryptostemma*, but is differentiated from the latter not only structurally but also by biotope preferences. Its distribution is incompletely known; the published records are from the W Palaearctic and the C Asia, but I also have at my disposal several new species from the Neotropical region, collected at light near high mesas in Venezuela. In the W Palaearctic we have *Pachycoleus utnapishtim* (Linnavouri) whose single specimen was collected at light in Iraq, and two European species (with somewhat uncertain nomenclature *P. waltlii* Fieber from N and C Europe, and *P. pusillimus* (J. Sahlberg) also from N and C Europe and with unverified records from Corsica and Greece; at least we know that the genus is distributed probably all over the European Mediterranean.

2.3.2. Biology

Data on habitat preferences and biology of *Pachycoleus* and *Cryptostemma* are admittedly incomplete and surely too sweeping, since my extensive material has yet to be identified as to species, and early spring samples are not available as on all occasions the suitable biotopes were flooded when visited. Both genera occur in different habitats. The European

* The identity of *Pachycoleus rufescens* (J. Sahlberg) should be re-examined.

Pachycoleus species are never associated with streams, while *Cryptostemma* species occur on (or rather in) banks of streams.*

Three major habitats of *Pachycoleus* were identified, always with *Hebrus ruficeps* as an associated species. (a) Mats of very wet *Sphagnum* (often also partly submerged in pools) as described for *Ceratocombus* sp. A, with the same associated heteropteran species, occured not only in bogs but also in fens. Population density is always low. (b) Thin and loose growths of hygrophilous mosses among low sedges on moist but not too muddy ground along gentle banks of clear water basins, in association with both common *Hebrus* species and common *Saldula* species. Berlesating yields good results. In Czechoslovakia such habitats occur mainly along large artificial fish-ponds in lowlands; their water is now mostly poluted by fertilizers and *Pachycoleus* seems to have disappeared from this biotope. (c) The main and reliable biotope is found in lowland fens in small mounds ("Bulten" in German) formed by *Sphagnum* and hygrophilous true mosses in swamps around tussocks of grasses, sedges, *Comarum palustre* and *Vaccinium uliginosum*; the same habitat was identified by BENICK (1920). Berlesating *Sphagnum*, mosses and litter particularly at the transition zone between wet and dry parts of these mound may yield numerous specimens, but although *Pachycoleus* regularly lives here, it occurs in agglomerations and the result of sampling is unpredictable. At no locality have I been able to collect samples throughout the year and hence I am not sure about the life cycle. This habitat is often flooded for weeks and the bugs must survive under water. *Hebrus ruficeps* is always abundantly present, and also *Chartoscirta*, *Rhopalus maculatus*, and *Ligyrocoris* and *Pachybrachius* larvae occur heere.

All species of *Cryptostemma* inhabit interstitial spaces formed by gravel and sand along the banks of a stream. They live in truly edaphic, lithophilous situations and although I have collected numerous specimens and spent a long time in this biotopes I have never encountered a single individual on open ground. The adults are attracted to light in the tropics (I have no experience in this respect) and aerial dispersal surely occurs at night in temperate regions. (Even diurnal dispersal may occur under unusual circumstances; S. DROSOPOULOS (pers. comm.) recalls an occasion when dozens of *Cryptostemma* adults landed at the water surface and on his body during a day in a flooding stream in Greece). Only individual collecting is advisable, berlesating is an unsuitable method. The type of stream does not seem to be important, suitable macrobiotopes range from

An exception to this rule may be the Central Asiatic *Pachycoleus gracilis* (Josifov) since the localities of the type series indicate collecting along a river; however, no details are known. A single case of the occurence of *Cryptostemma* on a lake shore is mentioned below.

small mountain brooks to large, fast or slow lowland rivers, but several conditions are necessary: (a) The water must be clean, well oxygenated, without an excessive load of agricultural and industrial polutants *Cryptostemma* habitats are subjected to long periods of flooding in early spring and any time after heavy rains, and the bugs do not leave their habitat and use plastron respiration during such periods. (b) Suitable riparial habitats formed by accumulated stones, pebbles, gravel and sand, and not fully covered by vegetation, must be available at banks or on river islands. It would be futile to search for *Cryptostemma* along streams with banks formed by the usual types of soil, mud, loess or pure sand. (c) The habitats should not be excessively splashed and must not be permanently shaded, which that very fast mountain or rocky streams as well as deep creeks in forests are excluded. (d) The individuals of *Cryptostemma* can live under large stones or pebbles, among rough gravel or inside the terraces formed by pebbles and gravel, and the ground may be formed (or spaces among larger stones filled) by sand, soil, or silt, but only in such a way that many narrow interstitial corridors not filled by water are available. The ground may be actually "muddy", but free interstices must remain there. High humidity of the microbiotope is necessary, but the adults may occur also in dry sites nearby. In high riparial terraces one can easily identify the humid zone prefered by *Cryptostemma* and situated betweenthe dry upper layer and the lower one with interstices filled by capillary water. Vertical migration of the populations according to the changing water level is also noticeable.

Exceptionally, *Cryptostemma alienum* may occur in gravel terraces not associated with streams. A. & M. GOGALA (pers. comm.) collected this species in Yugoslavia on the banks of mountain lakes (Krnsko jezero, Bohinjsko j.) with a fluctuating water level, in a microbiotope corresponding in all essential points to those described above.

In Czechoslovakia and S Poland it is possible to find active adults and larvae of all instars throughout the year, approximately from the beginning of May to the beginning of November. I assume tentatively that *Cryptostemma* species are acyclic, and hibernate both in the larval and adult stage, and possibly even in the egg stage. However, I have not succeeded in finding hibernating individuals and do not know anything about the early spring populations since all the localities I have visited are regularly flooded at that time of year. I have no idea about voltinism either. Small, semi-isolated demes generally within the same locality, investigated at the same date, often show markedly different stage/instar compositions; this seems to suggest dependence on the instar in which the founding female hibernated and(or) an extremely protracted oviposition. Species- specific or regionally different life-cycles (and possibly also habitat preferences) may of course occur in *Cryptostemma*, but no data are available so far; however, my experience warns against drawing conclusions from small samples.

A few notes on the behaviour of *Cryptostemma* should be added; they are based on both field and laboratory observations. Both larvae and adults are photophobic, very agile, and when they are exposed they immediately show a marked escape reaction. They either immediately run into narrow interstices in the ground, or the adults may first combine escape jumps, runs and flights. If they accidentally land on a water surface they float for hours or even days, touching the surface film only by the apices of their legs, labium and sometimes abdomen. Their body never gets wet. The individuals observed on the substrate groomed their body practically all the time using all three pairs of legs, also rubbing perpetually the surface of the abdomen and forewings. I suspect that not only cleaning is involved but that the main purpose is the spreading of a hydrophobic secretion (source unknown - scent glands?) over the body.

When *Cryptostemma* individuals are submerged, a plastron film that may combine with a large air bubble develops immediately over their bodies. In one extreme a thin plastron layer continuously develops over the dorsum of the body and the venter of abdomen of both larvae and adults, in another (adults) the whole insect is "enwrapped" in a large, drop-like air bubble that envelopes particularly the abdomen, including the subalar space. When submergence occurs while the individual is on the substrate, it either remains immobile on the spot or creeps into the nearest crevice. Submerged individuals survive for weeks, and I believe that true plastron respiration is involved. I do not know whether in natural situations survival is ensured largely by this aquatic respiration, or by remaining in shelters formed by air bubbles trapped in the interstices.

Cryptostemma species live in biotopes whose upper layers are frequented by many coleopterans and their larvae (especially carabids, staphylinids, heterocerids and dryopids), lycosid spiders, mites and collembolans; *Macrosaldula scotica* and *M. variabilis* occur frequently on the surface. Both larvae and adults of *Cryptostemma* exhibit continuous searching behaviour, touching the ground all the time with the apex of the rostrum. I suppose that the main source of their food in interstices must be collembolans and mites (and possibly the ubiquitous nematodes and chironomid larvae), since no other macroscopic animals were found in some habitats. C. Rieger (pers. comm.) saw the adults feeding on bodies of dead mayflies in FRG. No predators of *Cryptostemma* have been recorded, but I. KERZHNER (pers. comm.) is of the opinion that *C. japonicum* Miyamoto in the Far East is preyed upon by *Boreostolus sikhotalinensis* Wygodzinsky and Štys (Aenictopecheidae), a rare enicocephalomorphan sharing the same habitat.

I am still puzzled by one aspect of the life of *Cryptostemma*. Despite many hours of observations in the laboratory and hundreds of hours spent collecting I have never encountered a copulating pair, although one would assume that copulation in species with extremely elaborate male pregenital

and genital structures would be long rather than short. The same applies to *Pachycoleus* and *Ceratocombus* species, although I have not had such ample opportunity to observe them. Actually, the method of copulation has not yet been described in any species of the Dipsocoromorpha and Enicocephalomorpha. It is a pity, since in both these critical groupsunusual genitalia, terminalia and male pregenital and postgenital structures frequently occur (ranging from extremely simple to extremely complex, often with many plesiomorphic components), and there is no functional interpretation for the many curious structures. For instance, the function of male genital and pregenital laterotergal appendages and other group-specific male abdominal structures is entirely unknown in the Dipsocoromorpha, and this group exhibit a strange trend: the more elaborate are the male terminalia and abdomen, the simpler and more reduced is the situation in conspecific females. To illustrate the point: the male of the schizopterid *Semangananus mirus* Štys possesses an unusually complex pregenital abdomen bearing even a large pregenital secondary copulatory organ, which is a unique case among all neopteran insects; its female has no external genitalia, just a big hole.

I should like to stress that *Cryptostemma* (as well as other Palaearctic dipsocoromorphan genera) seems to be a promising and rather easily available experimental model for finding many new facets of heteropteran biology. I have never tried hard to establish cultures; anybody who is interested and can spare the time should be encouraged to study the biology of these bugs in more detail and under proper experimental conditions.

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