Splitting by adaptive traits in the *Rhyacophila obscura* species group (Trichoptera, Rhyacophilidae)

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Abstract. The discovery of two new sibling species of the *Rhyacophila obscura* species group in the same population from the Fan-Si-Pan Mts. of Vietnam and the detected shape divergences of paraprocts with speciation trait function of reproductive barrier building initiated the survey of the entire species group. Character tree discordances inside the species tree motivated and justified us to survey briefly some aspects of splitting theory and practice. At all levels of taxonomic hierarchy there are genealogical discordancess. Every homologous phenomic trait or nucleotide position may have their own true tree-like history. How taxonomists try to create nominal kinds most corresponding to the natural kinds along the iterative fractal splitting. Fractal is the nature’s geometry and organises itself by the negentropy of integration and reticulation against the entropy of disintegration. Splitting along fractals and reticulation produces independent adaptive or neutral genealogically discordant trees; therefore, the reality of phylogenetic trees is highly questioned. Pheneticists work with large set of unweighted characters and without real hermeneutic analysis. Applying large number of unweighted adult, larval or molecular characters of independent tree histories and without hermeneutics we kill the reality of splitting. In the genealogy of *Rhyacophila obscura* species group we have applied weighted characters in lineage splitting by the hermeneutics of adaptive/neutral, commonality/generalility, distribution/area and complexity/simplicity principles. *Rhyacophila obscura*, the ancestral species of the species group has (1) the most robust/complex adaptive epiproct and paraproct, the traits liable to adaptive divergences in reproductive isolation; (2) the most common/general distribution of the adaptive ancestral epiproct in the complex; (3) and the largest distributional area. This ancestral species was diverged to *R. bidens*, to the ancestor of the complex splitted by the reduction of epiproct to a small bilobed structure. The ancestral complex of *R. obscura* and the first splitted complex of *R. bidens* have been further splitted both by contemporary adaptive paraproct reduction and by neutral stochastic shape divergences of segment X and harpagones. During these splitting practices four new species were described: *R. assamensis* sp. nov., *R. atlagos* sp. nov., *R. kurna* sp. nov., *R. sudar* sp. nov.

Keywords. Trait tree, species tree, splitting principles, new species.

INTRODUCTION

A marbled-winged and medium-sized *Rhyacophila* species was collected (population sample of 53 males, 21 females) by Canadian zoologists in the Fan-Si-Pan Mountains of Vietnam, deposited in the Royal Ontario Museum (ROM) and identified as *Rhyacophila bidens* Kimmins (Armitage & Arefina 2003), a widely distributed ancestral taxon of the small *Rhyacophila obscura* species group. Initially, we studied two other male specimens with similar habitus collected by Hungarian zoologists from nearby habitats in the Fan-Si-Pan Mountains of Vietnam and deposited in HNHM. Surprisingly the fine phenomics of the two specimens was different: we have detected remarkable divergences in the fine structures of their paraprocts. Borrowing and examining with fine phenomics the paraproct structure of 44 specimens from ROM, identified as *R. bidens*, revealed that these specimens represent the same two undescribed species with similarly subtly, but stably diverged paraprocts. The possibility that the detected shape divergences of paraprocts may function as a speciation trait of reproductive barrier building has initiated this study. We planned to examine the shape divergences of paraprocts by focus on fine phenomics, as the initial split criteria for species delimitation in this species group. We put to-
Splitting theory and practice

In general the detection of shape divergences in speciation traits requires the application of both the principles and practices of fine phenomics. Its arsenal and essence are not limited just to higher magnification. Most important is that focused due attention must be directed to traits of reproductive structures with subtle and stable divergences. It routinely includes and requires careful empirical practice and hermeneutics on (1) character selection; (2) character analysis; (3) character ranking; (4) screening possible supertraits involved in reproductive isolation; (5) fine cleaning and clearing of genitalia; (6) adequate microscopic resolution; (7) comparative and proper selection of the examination view for trait presentation and drawing; (8) variability range detection for adaptive/neutral distinction. By proper application and further development of fine phenomic there exists a real potential to detect stable shape divergences in the early reproductive barrier building enabling us to delineate incipient sibling phylogenetic species by the initial splitting criteria. This is confirmed here by delineating incipient species by speciation trait of paraproct in the Rhyacophila obscura species group. Young species delimited either by virtual neutral sequences or by empirical speciation traits are exposed to traditional debates between splitters of differences and lumpers of similarities. However, not the taxonomists, but the universe itself splits the entities of nature in an iterative fractal mode by integrative organisation (Oláh et al. 2018). Taxonomists try establishing nominal kinds, the taxa most corresponding to the natural kinds of this fractal splitting.

Splitting along fractals. Anything is fractal if the new outgrowths are proliferating by iteration principle like river networks, plant trees, phylogenetic trees or human vascular system (Oláh et al. 2017). Fractal splitting, being iterative, contains and reflects its own semantics, almost self-explanatory. The gross taxonomy, our present nominal kinds rely upon principle that divergence (splitting the lineages) occurs in nature, in spite of reticulation (melding of lineages). But in nature, reticulation dominates over divergence and integration over selection according to the general organisational system: aggregates of element in interaction (Botnariuc 1967). Both the reticulation and divergence, like the nature itself, are organised in fractal pattern. These iterative mechanisms occur and function along the largest and along the smallest, irreducible cladistic units. Fractal is the nature’s geometry and organises itself by the negentropy of integration and reticulation against the entropy of disintegration (Oláh et al. 2018).

Independent spontaneous splitting. All taxa are a mix in various rations of ancestral and derived characteristics (Omland et al. 2008). These classical entities are composed of quanta and are the results of quantum mechanisms. They are products (1) of einselection (Zurek 2003); (2) of the environment induces decoherence, when entangled particles decohere; (3) of the collapse of wave-packet superposition along a single eigenstate with known eigenvalue. Taxa are products from the probability cloud of gene/trait trees in species trees. It seems that interacting with the environment splits the world along fractal iteration on all level of organisation. Under the permanent external and internal perturbation pressures there is a counteracting comparative balancing power of integrative organisation to sustain structural and functional autonomy in every once-emerged entity. These protective mechanisms may function by reinforcement like inverse barriers in quantum tunnelling, and they are more elaborated for adaptive traits and less effective for neutral traits. As a result neutral traits are more exposed to stochastic pressures of random effects and the single or various packages of combined characters could be randomly and independently ancestral or derived. Nevertheless, the most adapted stochastic splitting is the end product of speciation supervised by the balancing power of the integrative organisation. As a result at all levels of taxonomic hierarchy there are genealogical discordances, every homologous phenomic trait or
nucleotide position may have their own true tree-like history. The reality of dichotomic (or polytomic) phylogenetic trees is highly questioned, they are almost certainly reticulated (Oláh et al. 2018).

Splitting principles. Characters should not have equal value in phylogenetic analysis. But they usually have! Pheneticists work with large set of unweighted characters and without real hermeneutic analysis. Unweighted splitting, dominates in numerical taxonomy and in molecular sequence processing, remains blind without empirical hermeneutics. The phenetic species concept in taxonomy and phenetic clade construction in systematics do not give adequate importance to apomorphic characters of “evolutionary novelties”. Applying large number of unweighted adult, larval or molecular characters with independent tree histories without hermeneutics we kill the reality of splitting.

Splitting practices. In this small species group we apply a simple demonstrative approach to reconstruct the possible splitting histories by empirical phenomics. We decide upon temporal sequences of splitting by character ranking of empirical parsimony in hermeneutics with the help of universal principles (Winther 2009, Schmitt 2016, Oláh et al. 2017) of (1) commonality: common equals primitive, character state present in the largest number of taxa is plesiomorphic; (2) generality: hierarchical concept: character state present in the entire group is plesiomorphic relative to alternative character state of a subset of that group; (3) complexity: following Williston (1914), Gregory (1935) and Schmid (1979): complex is plesiomorphic, calculating that complexity could arise, not only by incremental addition but by incremental subtraction (Oláh et al. 2014): the reduction in the number of structural parts could be associated with increasing complexity (Esteve-Altava et al. 2013); (4) locality or area: larger distributional area is accompanied with plesiomorphy, especially with peripatric siblings; (5) distinction between adaptive and neutral traits: subtle and stable adaptive contemporary divergences. We use an empirical synthetic method for character definition by combining observed conditions along examined entities gained with analysing character by character or taxa by taxa based on observed ranges of variations obtained from population samples.

Splitting in Rhyacophila obscura group

Rhyacophila obscura Martynov, 1927 was described from the region of “12 sources”, 75 km NE from Tashkent, Uzbekistan as related, though not closely, to Siberian species of R. depressa Martynov, R. sibirica McLachlan and R. lenae Martynov (Martynov 1927). In his seminal study on joint treatment of the evolution and classification Ross (1956) has placed R. obscura together with R. bidens Kimmins, R. scissa Morton and R. scissoides into the R. scissa species group as an offshoot of R. castanea stem (Ross 1956). In his canonical study on the entire genus Schmid (1970) has removed R. obscura together with R. bidens from the R. scissa species group and placed them into the newly established R. obscura species group in the R. castanea stem of R. philopotamoides branch together with three new species R. chenmo, R. chungse and R. sakyapa.

Schmid (1970) has recognised that the epiproct (anal sclerite of Schmid) and the harpagones, the second segment of the gonopod split independently in this species group. The combination of these dis harmoniously splitted traits has the power to delineate species, but result in different trees. The tree of epiproct shows dissimilar phylogenetic relations compared to gonopod tree. These discordant trait trees obscure lineage sorting. Which trait tree represents the species tree? The discordance created by different phylogenies of the different trait trees were absolved by giving higher ranking value to epiproct splitting. Theoretically he has based and constructed his species tree of the group on the epiproct tree and the gonopod splitting was considered secondary as a result of parallel evolution.

As we have discussed, in spite of the integrative organisation, unknown ratio of traits or trait
aggregates may split independently and spontaneously in random, non-synchronous pattern. We agree with Schmid’s construction of phylogeny giving higher splitting value to epiproct, but he has selected this option without any explanation or interpretation. Why he has given higher splitting value to epiproct is not communicated. Our hermeneutics is based upon the ranking/splitting principle of adaptive/neutral distinction. We have given higher importance in lineage splitting to epiproct and paraproct due to their adaptive divergences. The gonopod shape divergences were considered as neutral and random process driven, mostly stochastic product of integrative organisation against external and internal environmental impacts, realised under the random mechanisms of mutation, permutation, transmutation, perturbation, effective population size, gene flow, genetic drift, and recombination. Lineage splitting, the decision about the phylogenetic ranking value of the diverged traits in the *Rhyacophila obscura* species group was implemented by applying our principle of adaptive/neutral trait distinction in combination with the commonality/generality, complexity and locality/area ranking/splitting principles.

*Rhyacophila obscura*, the ancestral species of the species group has (1) the most robust/complex adaptive epiproct and paraproct, the traits liable to adaptive divergences in reproductive isolation; (2) the most common/general distribution of the adaptive ancestral epiproct in the complex; (3) and the largest distributional area. This ancestral species was diverged to *R. bidens*, to the ancestor of the complex splitted by the reduction of epiproct to a small bilobed structure. The ancestral complex of *R. obscura* and the first splitted complex of *R. bidens* have been further splitted both by contemporary adaptive paraproct reduction and by neutral stochastic shape divergences of segment X and harpagones.

*Rhyacophila obscura*, the ancestral complex. This complex has larger distribution area from Iran to Vietnam as compared to the *R. bidens* complex with more limited distributional area from India (Garhwal) to Myanmar. All lineages have large epiproct and further splits are produced by adaptive paraproct reduction in sexual integration of reproductive barrier building or by random shape divergences in neutral traits of segment X and gonopod.

1. The nominate species represents the ancestral lineage of the species group with large reniform, subtriangular epiproct and large clavate paraproct and highly bilobed harpago. *R. obscura*: distributed from Iran to Myanmar.

2. Subtriangular epiproct retained. Contemporary splitting by adaptive paraproct reduction is accompanied by the reduction of the dorsal lobe on the neutral trait of harpagones of gonopod. *R. atlagos* sp. nov. *R. kurta* sp. nov.; both new species diverged in the Fan-Si-Pan Mts. Vietnam.


*Rhyacophila bidens*, the first splitted complex. This complex is distributed from India (Garhwal) to Myanmar. Its all lineages have small reduced epiproct with bilobed shape and further splits are produced either by adaptive paraproct reduction in sexual integration of reproductive barrier building or by random shape divergences of harpagones.

1. First ancestral splitting from *R. obscura* by epiproct reduction: *Rhyacophila bidens*.

2. Contemporary splitting from *R. bidens* by paraproct reduction: *R. sudar* sp. nov.

3. Splitting by neutral trait of gonopod: *R. chungse*.

4. Contemporary splitting from *R. chungse* by paraproct reduction accompanied by neutral trait splits in segment X and harpagones: *R. amatulla* sp. nov.

MATERIALS

To examine the fine structure of the paraproct we have borrowed type materials, holotype and paratypes of *Rhyacophila bidens* Kimmins, 1953 from the Swedish Museum of Natural History, as well as one paratype of *R. bidens* from the Canadian National Collection; paratypes of *R.
chenmo Schmid, 1970, R. chungse Schmid, 1970 and R. sakvapa Schmid, 1970 from the Canadian National Collection as well as holotype of R. szaboi from the Mátra Museum of the Hungarian Natural History Museum. Non-type materials of R. bidens were borrowed from Royal Ontario Museum determined by Brian Armitage and from the Canadian National Collection determined by Fernand Schmid. Specimens from Nepal were available from Kiss Private Collection and the two specimens from Vietnam, those initiated this study were received from the Hungarian Natural History Museum.

**Depositories.** Canadian National Collection, Ottawa, Canada (CNC); Kiss Private Collection (KPC); Mátra Museum of the Hungarian Natural History Museum, Gyöngyös, Hungary (MM); Oláh Private Collection, Debrecen, Hungary, under national protection of the Hungarian National History Museum (OPC); Royal Ontario Museum, Toronto, Canada (ROM); Swedish Museum of Natural History, Stockholm, Sweden (SMNH)

**TAXONOMY**

*Rhyacophila assamensis* sp. nov.

(Figures 1–4)

*Rhyacophila chungse* Schmid, 1970:152. 5 paratypes: India, Assam, Kameng, from five localities. The holotype is described from India (Manipur). The 5 paratypes from Assam proved to represent a diverged distinct new species. Misidentification!

**Material examined.** Ho


**Diagnosis.** A member of the R. bidens complex. A new species of the contemporary splitting from R. chungse by paraproct reduction accompanied by neutral trait splits in segment X and harpagoes. *R. assamensis* sp. nov. is most close to *R. chungse* Schmid, 1970, but differs by having filiform paraproct in caudal view, not the ancestral form of clavate paraproct; epiprost is widely bilobed, not narrow; the neutral trait of segment X tapering triangular, not digitate both in dorsal and ventral view; the neutral trait of harpagoes bilobed and the ventral lobe broad, not slender.

**Description.** Male (in alcohol). Body, appendages and wings brown, maxillary palp formula I-II-IV-V-III, forewing length 11 mm; forewing mottled, thyridial spot conspicuous, small hyaline spot visible on the margin of the apical cells.

**Male genitalia.** Segment IX is longer dorsad than ventrad. Segment X as long as wide with rounded triangular excision in dorsal view; small bilobed epiproct (anal sclerite) present and the mesal and lateral lobes widely separated; paraproct composed of tergal strap and sclerotized U-shaped apical band with reduced, slim filiform median lobe. Gonopod bisegmented; harpagoes bilobed, ventral lobe longer almost as broad as the dorsal lobe. Phallic organ composed of phallobase (short phallotheca and most developed endophalange), aedeagus and parameres; parameres stout erectile processes, capitulate by short dorsal and long ventral setae; phallothecal tenon and gonopodal tendon well developed; aedeagus with single dorsal and bifid ventral arms.

**Etymology.** Named after the locus typicus.

*Rhyacophila atagos sp. nov.*

(Figures 5–8)

Diagnosis. A member of the *R. obscura* ancestral species complex having the retained sub-triangular epiproct present. Contemporary splitting by adaptive paraproct reduction is accompanied by the reduction of the dorsal lobe on the neutral trait of harpagones of gonopod. *R. atlagos* sp. nov. is most close to *R. kurta* sp. nov. but differs by having segment X wider than long; harpagones with less excised, not step-wise apical margin in lateral view; median lobe on paraproctal complex abbreviated to a medium-sized plate, not lost.

Description. Male (in alcohol). Body, appendages and wings brown, maxillary palp formula I-II-IV-V-III, forewing length 11 mm; forewing mottled, thyridial spot conspicuous, small hyaline spot visible on the margin of the apical cells.

Male genitalia. Segment IX longer dorsad than ventrad. Segment X shorter than wide with short V-shaped excision in dorsal view; subtriangular epiproct (anal sclerite) present; paraproct composed of tergal sclerite and robust sclerotized U-shaped apical band with medium-sized plate-like median lobe. Gonopod bisegmented; harpago
Elongated. Phallic organ composed of phallobase (short phallotheca and most developed endotheca), aedeagus and parameres; parameres stout erectile processes, capitate by short dorsal and long ventral setae; phallothecal tenon and gonopodal tendon well developed; aedeagus with single dorsal and bifid ventral arms.

**Etymology.** atlagos from “átlagos” average in Hungarian, refers to the average size of the median lobe (lingua at Schmid) of the paraproctal complex (apical band of Schmid).

**Rhyacophila bidens** Kimmins, 1953

*Material examined. Holotype. Myanmar*, N. E. Burma, Kambaiti, 7000 ft., 30.IV.1934, R. Malaise. The entire holotype is mounted in single permanent slide: 4 wings, abdomen, right gonopod and rest of the body, deposited in SMNH.

Distribution. Myanmar, India (Garhwal, Manipur, Assam, Sikkim), Nepal

Rhyacophila chenmo Schmid, 1970


Rhyacophila chungse Schmid, 1970


Rhyacophila kurta sp. nov.

(Figures 9–12)

Rhyacophila bidens Kimmins, 1953. Armitage & Arefina 2003: 114–116. Among the examined 44 male paratypes we have found 35 R. kurta sp. nov. and 9 R. atlagos sp. nov. specimens. The drawings are probably from a specimen of R. kurta. Misidentification!


Diagnosis. A member of the R. obscura ancestral species complex having the retained sub-triangular epiproct present. Contemporary splitting by adaptive almost complete paraproct reduction is accompanied by the reduction of the dorsal lobe on the neutral trait of harpagones of gonopod. R. kurta sp. nov. is most close to R. atlagos sp. nov. but differs by having segment X longer than wide; harpagones with more excised, stepwise apical margin in lateral view; median lobe on paraproctal complex abbreviated, almost lost, not a medium-sized plate.


Male genitalia. Segment IX longer dorsad than ventrad. Segment X longer than wide with rounded excision in dorsal view; small triangular epiproct (anal sclerite) present; paraproct composed of tergal strap and robust sclerotized U-shaped apical band with abbreviated median lobe. Gonopod bisegments; harpgone short with stepwise apical margin. Phallic organ composed of phallotheca (short phallotheca and most developed endotheca), aedeagus and parameres; parameres stout erectile processes, capitae by short dorsal and long ventral setae; phallothecal tenon and gonopodal tendon well developed; aedeagus with single dorsal and bifid ventral arms.

Etymology. kurta from “kurt” short in Hungarian, refers to the abbreviated very short mesal lobe (lingua at Schmid) of the paraproctal complex (apical band of Schmid).

Rhyacophila obscura Martynov, 1927

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Figures 9−12. Rhyacophila kurta sp. nov. Holotype male: 9 = segment X, epiproct and paraproct in lateral view; 10 = segment X in dorsal view; 11 = segment X, epiproct and paraproct in caudal view; 12 = left harpago in lateral view.


Remarks. Widely distributed species reported from Iran, Pakistan, China (Xinjiang), Nepal, Bhutan, Kazakhstan, India (Himachal Pradesh) and here we report it from Afghanistan and Myanmar.

Rhyacophila sakyapa Schmid, 1970


Diagnosis. Having small bilobed epiproct R. sudar sp. nov. is a member of the R. bidens complex. A new species of the contemporary splitting from R. bidens by adaptive paraproct reduction accompanied by neutral trait splits in segment X and harpagones. R. sudar sp. nov. is most close to R. bidens Kimmins, 1953, but differs by having highly reduced filiform and abbreviated paraproct in caudal view, not the ancestral form of clavate paraproct of R. bidens; the neutral trait of segment X rather digitiform both in dorsal and ventral view, not tapering triangular; the neutral trait of harpagones with lower and longer dorsum.
Description. Male (in alcohol). Body, appendages and wings brown, maxillary palp formula I-II-IV-V-III, forewing length 11 mm; forewing mottled, thyridial spot conspicuous, small hyaline spot visible on the margin of the apical cells.

Male genitalia. Segment IX is longer dorsad than ventrad. Segment X longer than wide with rounded triangular excision in dorsal view; small bilobed epiproct (anal sclerite) present and the mesal and lateral lobes well separated; paraproct composed of tergal strap and sclerotized U-shaped apical band with reduced, slim filiform median lobe. Gonopod bisegmented; harpagones monolobed, dorsum low and long. Phallic organ composed of phallotheca (short phallotheca and most developed endotheca), aedeagus and parameres; parameres stout erectile processes, capitate by short dorsal and long ventral setae; phallothecal tenon and gonopodal tendon well developed; aedeagus with single dorsal and bifid ventral arms.

Etymology. sudar from “sudár” slender, slim in Hungarian, refers to the slim median lobe (lingua at Schmid) of the paraproctal complex (apical band of Schmid).

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Figures 13−16. Rhyacophila sudar sp. nov. Holotype male: 13 = segment X, epiproct and paraproct in lateral view; 14 = segment X in dorsal view; 15 = segment X, epiproct and paraproct in caudal view; 16 = left harpago in lateral view.

REFERENCES


