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The distribution of *Hemiragis aurea* (Brid.) Ren. & Card. (Hookeriaceae, Musci) and related notes of interest

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Abstract: The horizontal and vertical range of *Hemiragis aurea* (Musci) is subdivided into four regions: I - N. Panama, Costa Rica, S. Nicaragua; II - circum-Caribbean; III - Guyana Highlands; IV - Andean. Ecological evidence is discussed in the context of the effects of volcanic eruptions, hurricanes, climactic changes and other factors.

Introduction

Hemiragis aurea (Brid.) Ren. & Card. is one of the noteworthy components in the Neotropic bryo-flora because of its uncertain affiliation to higher taxonomic units, its extraordinarily differentiated distribution, and its pronounced ecological amplitudes. The distribution of *H. aurea*, along with other mosses which are similarly limited to the Neotropics and have matching ranges, shows some connection with the geological history of the Neotropics. This relationship cannot be satisfactorily interpreted unless the factors responsible for the origin of these phenomena are causatively and properly recognized, and for this reason this taxon is worthy of detailed studies.

Remarks on Distribution

The distribution of *Hemiragis aurea* can be arranged in the following four groups and is presented in Fig. 1.

I. The Central American region includes N. Panama, Costa Rica, and S. Nicaragua (Guatemala?), with many localities from ca. 200 m alt. along the Atlantic coast up to 1700 m inland. An Atlantic lowland occurrence on the Panamanian isthmus belongs to region II (see below) and is probably separated by a narrow distribution gap from the inland occurrence in the mountains. The unpublished localities from

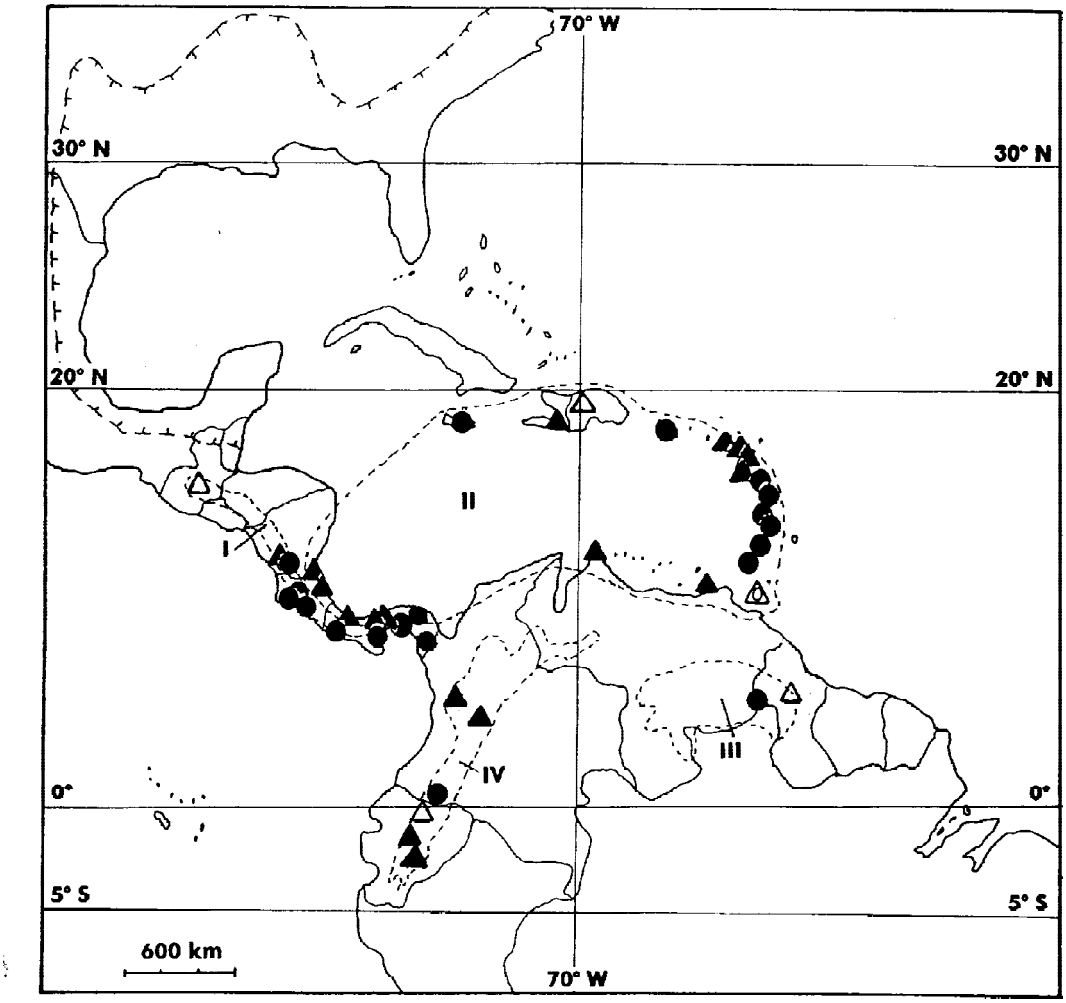

Fig. 1. Distribution of *Hemiragis aurea*: (dots) single locality; (triangel) group of localities; (open triangel) unspecified locality; I-IV - regions (see text); (hatched) sea level at end of the Cretaceous (Benton & Little, 1994).

region I are:

Panama. Fortuna Dam Site, top of mountain, 1700 m, on tree, coll. J. P. Folsom, K. & D. Dressler #5423 (H); as above, 800 m, on overhanging branch, coll. B. Allen #5866 (MO); NW Santa Fé, 2.7 km from Escuela Agricola Alto de Piedra, on twig, coll. S. Mori & J. Kallunki #5366 (MO); as above, along Rio Caloveborita, 11 km N of Santa Fé, Atlantic slope, 450-500 m, tropical wet forest on slopes, coll. unknown, 1986 (MO); Bocas del Toro Prov., Cerro Colorado, 1400-1470 m, near the top of ridge, on trunk, coll. B. Allen #5112 (MO); Coclé, El Valle de Anton, coll. McPherson #7658B-5 (MO); Comarca de San Blas, Cerro Habú, coll. Sytsma et al. #2703 (MO); Darién, Cerro Pirre, coll. Folsom #4488 (MO).

Costa Rica. Prov. Cartago, 15 km S. of Tapanti along Rio Grande de Orosl, ca. 1600 m, boulders and rocks at edge of forest along river, coll. M. Nee, R. Kowal, T. & B. Cochrane #14381 (MO); Cartago-Reserv. Forest, Tapanti, 1340-1600 m, on very moist rock, coll. D. Griffin III, M.J. Morales, D.E. de Retana #193 (FLAS); La

Hondura, Prov. San José, 1300-1700 m, coll. P.C. Standley #36547 (CANM - duplicate).
Nicaragua. Dept. de Rivas, Isla Ometepe, Laguna Volcan Maderas, ca. 440 m, coll. P. P. Morerro #19781 (CANM); Dept. Granada, Volcan Mambacho along W. shore of Lake Nicaragua, ca. 15 km from Granada, 1100 m, coll. T.B. Croat #39147 (CANM).
In Guatemala *H. aurea* is known from only a single, general report ("Guatemala, 1841 - leg. Fiedrichsthal", H, without no.) published by Mueller (1897) as "H. friedrichsthaliana - sine loco natali" and revised by Britton (1914). Its presence in Guatemala is questionable due to the absence of specific locality information and the fact that it has never been recollected in that country.

II. The circum-Caribbean region consists of localities on the islands, the northernmost portion of South America and the east coast of the Central American isthmus. The following are comments on published reports and remarks on unpublished findings from this region:
Jamaica (max. alt. Blue Mts. - 2256 m). Many localities from ca. 700-1600 m. The lower altitudinal limit on the SW. slopes of the Blue Mts. as per Crum & Bartram (1958) is about right according to my observations in 1980.
Hispaniola (max. alt. Pico Duarte, 3175 m): Dominican Republic - general report without a locality (Welch 1972); Haiti - "Massif de la Hotte, Parc National Pic Maraya, Bois Formon. Disturbed moist forest on limestone, alt. 950-1040 m, leg. W. S. Judd, no. 3557" (FLAS).
Puerto Rico (max. alt. El Yunque, 1065 m). Many localities spread over the island from approximately 600 m up to summits.
Saba. An old state cited on the herbarium voucher labelled as "Guyana" (Guiana Batava) based on the collection described as "Juringeria guianensis....Guian, Saba, April 1886. coll. Suringar #623 (H), renamed as *Hemiragis striata* probably by V. F. Brotherus. See also Gradstein & Hekking (1989).
St. Kitts (max. alt. Mt. Misery, 1156 m). One general report (Welch 1972). This island has large non-arboreal spots of vegetation on its summits and the occurrence of *H. aurea* there is analogous to the next locality.
Nevis. "At summit (985 m - M. K.) and on adjacent ridges" (Welch 1972, p. 424). There are two summits occupied by non-arboreal, partly shrubby, very dense vegetation with minor epiphytic growth, which is abundant just below it and continues to middle elevations, approx. 600-950 m.
Montserrat (max. alt. 914 m). "Chances Mountain" (Welch 1972), or "summit of Chance's Mt., Soufriere Hills, on trees" as per specimens #19119/1683 (CANM), between "2800-3000 ft.", coll. R. Proctor.
Guadeloupe. Many localities, all below Sans Toucher Mt. with the highest peak 1480 m. Lowest ones: dense growth at the river Classe Mateliane (Jovet-Ast 1946), Campesterre (Welch 1972), and Savane aux Ananas, lower part of tree, coll. P. Allorge #18 (P). See also ecological remarks below.
Dominica (max. alt. Morne Diablotin, 1447 m). Many localities scattered over the island. Both upper and lower limits cannot be considered as permanent after hurricane "David" in 1979 and probably previous ones; see remarks below concerning hurricanes. Unpublished localities: near Fresh Water Lake, in forest, 600-650 m, coll. M. L. Farr #1743 & 1732 (CANM); Parish St. George, between Laudat and Fresh Water Lake, on tree, 600-780 m, coll. E. & P. Hegewald #93980 (CANM); as above but between Fresh Water Lake and Boeri Lake, on tree, 780-800 m, coll. E. & P. Hegewald #9485 (CANM); near Laudat, coll. "Eggers s.n., II 1880", (H); and the author's unpublished material.
Martinique. Many localities, mostly at lower elevations, require altitudinal remeasurement. The highest areas below the tallest peak, Mt. Pelée (1463 m), are strongly eroded and there is, at present, no habitats suitable for *H. aurea*. The summit regions of Morne Jacob (750-884 m) are covered by relatively rich moss growth, especially abundant in wet places on extensive charcoal layers and burnt logs on which the species was not found. The first trees, mainly tree ferns, appear there in the valleys, but they are inhospitable for many epiphytes. As per observations made in 1979, the upper limit of *H. aurea* is at ca. 1000 m. It was reported from: Mt. Pelée - 1397 m (Bescherelle 1876), Morne Vert in Pitons du Carbet - 1160 m, Deux-Choux

- ca. 614 m, Balata - ca. 550 m, and others (see Welch 1972, p. 424). According to my observations a main occurrence lies between 300-1000 m, which agrees with Husnot's (1876) altitudinal limits of 500-1150 m for this species, confirmed by #187 of "Husnot, Pl. des Antilles - 1868". Unpublished herbarium localities: Mt. Pelée, ca. 300 m, coll. H. Stehle #3593 (CANM) and SE Mt. Pelée, Calebasse, abundant, 600-800 m, coll. P. Duss #23 (H).

St. Lucia (max. alt. Mt. Gimie, 970 m). NW. spur of Morne Gimie, ca. 920 m, "in mossy montane forest", coll. R. Proctor #17771/1631 (CANM); Gimie, Quarter of Anse-La-Ray, 733 m - the top, elfin woodland, coll. H. A. Imshaug #29844 (H) (also Welch 1972, p. 424).

St. Vincent (max. alt. Soufrière, 1234 m). Localities reported by Bartram (1956) and Welch (1972) from 300-1050 m require remeasurement after the volcanic eruption in 1979. See ecological remarks.

Grenada. At the highest peak St. Catherine Mt. - 840 m (Welch 1972 - based most probably on the collection in DS, coll. N. W. Simmonds #490, "epiphytic on *Didymopanax*, near summit of Mt. St. Catherine, 2700 feet"), also around the lake in the crater of Grand Etang slightly lower than above (unpubl. M. K.)

Trinidad (max. alt. Ario Mt., 940 m). An old general record never re-investigated: "Trinidad - leg. & det. Sieber" (in H without number or date, in MO with #20 on packet).

Venezuela. Two localities: Nueva Esperata on Isla de Margarita (914 m) and Falcon in Cerro de Santa Ana on Peninsula de Paraguana (650 - 700 m) - Griffin (1979).

III. The Guyana Highlands region, consisting of an inland complex of old mountains (many of which are table-shaped) from ca. 1000 m up to 2772 m in altitude.

Roraima Mt. (max. alt. 2772 m), 1200-1600 m, common on trunks and boulders (Gradstein & Florschütz-de Waard 1989). The locality cited by Florschütz-de Waard (1986), "Guyana: Jenman 7859 (BM, as *Harpophyllum*)...., near Demerara River", might be located in this region, since it was not found by the present author in the vicinity of Santa and The Bell, at the middle Demerara River and near Georgetown at the Atlantic.

IV. The Andean region includes Colombia and Ecuador and probably Bolivia from an altitude of several hundreds of meters up to 3000 m.

Colombia (max. alt.: Pico Simons, 5800 m). "Bogota" (2600-3000 m) - general old report (Britton 1914) republished many times as "Colombia" (according to Florschütz-de Waard & Florschütz 1979, and Churchill 1989 as "sine loco"); Alto del Veinte in Prov. Choco, 450-480 m (Churchill 1989, p. 120); northern vicinities of Lago La Cocha in Prov. Nariño, between El Encano and Paramo Bordoncillo, 2800-3000 m, collected and determined by M. Kuc in 1979 (specimens in COL).

Ecuador (max. alt. 6310 m). Abitagua Mt., 2000 m (Anonymous 1886, p. 74) in Prov. Tungurahua (cf. Mitten 1869, Steere 1948) and "Equador: Pipalto, coll. E. André #1394, 3 July 1880" (CANM); also "And. Quito", in "Spruce, Musci Amazonici et Andini", #712 (H). Welch's (1972, p. 424) statement: "*Hemiragis aurea*....Habitat (additional): altitude to 7200 m." is an error.

In Delgadillo et al. (1995) *H. aurea* is listed from Brazil and Bolivia. The Brazilian report is based on two collections by Sehnem: #4910a from Montenegro, documented by non-convincing illustrations (Sehnem 1979, Fig. IIB, 1-4) and #6414i from São Francisco de Paulo, (see also Yano 1981). Dr. D. M. Vital examined both of these collections and documented them by many exact *camera lucida* drawings (pers. comm.). In his opinion they belong to *Palamocladium leskeoides* (Hook.) Brid. The locality from Bolivia I was unable to trace in the literature.

For details regarding particular published localities see Bartram (1928, 1929, 1955, 1956), Breen & Reese (1971), Britton (1924), Britton & Williams (1914), Crosby (1967, 1969), Crum (1952), Crum & Arzeni (1953), Crum & Bartram (1958), Crum & Steere (1957), Mueller (1849-1851, 1897, 1898), Reed & Robinson (1971), Renauld & Cardot (1893), Welch (1971, 1972, 1974) and data cited in this paper.

The altitudinal range. Altitudinal data defines the range of *H. aurea* as narrow, attributed to

the loose, peripheral parts of tropical rain jungles and enclaves of rockland. On islands it ranges from tens of meters a.s.l. up to about 1700 m. In the inland mountains of the Central American isthmus and in the Andes it can be found from several hundred meters up to at least 3000 m with the main occurrence (in areas not disturbed by man, fire, volcanoes and others) between 400-1200 m. Both upper and lower limits are relative and difficult to specify because they are changed by many agents such as volcanic effects (ash, fire, erosion), hurricanes, coastal climates, and direct human and marine influences.

In this context it is surprising that the moss was not found on islands facing the open Atlantic, e.g., Barbados, Bahamas, or in the Pacific lowlands of the isthmian Central America or in the northern Caribbean. This phenomenon does not have an explanation in the light of present knowledge of plant geography.

Review of the bio-indices of *Hemiragis aurea*

All known detailed and generalized information about life requirements of *H. aurea* are based on field observations, responses to factors affecting it and the significance of morpho-anatomical structures. There are no chemo-physico or eco-physiological measurements devoted to this species.

The most accurate and comprehensive outline of its ecology was presented by Welch (1971, p.102). This, accompanied by more recently published data and my own observations, is as follows. *Hemiragis aurea* occurs exceptionally as an epiphyte on huge leaves (sic-bamboo, Jovet-Ast 1946) and herbs (Welch 1971), is rare on thin twigs, more common on branches and thinner trunks up to several meters above the ground and abundant on thick trunks, logs, rotten wood, snags, shrubs and as a bryochamaephytous to pseudo-epilithic moss occurs on boulders, organic soils and among dense (sometimes moist) growth of other bryophytes. Autecologically, it is a steno-photophilous, mesothermophilous (as a tropic moss), mesohygrophilous, nephelophilous, neutrophilous species; an obligatory lignicole, arboricole and facultative terricole. Synecologically, it is a member of epifolic, epiphytic, epixylic communities in epiphytic-epixylic niches and of bryochamaephytic ones in terrestrial niches. Both niches widely overlap one another. In view of negative ecocategories it is psychrofob, calci- and silicofuge, does not grow on barren, solid, smooth, vertical unweathered rock surfaces, and also avoids dark and permanently dry jungles.

Per its morpho-anatomical structures (gold colour, strong leaf plication, triangular appressed leaves, solid sclerotic anatomy of areolation and stems and others) it is a typical xerophyte, that contrasts with its occurrence in some wet, damp environments and its nephelophilic character. *Hemiragis aurea* is a typical anemogame frequently producing multi-sporecapsules, while its reproduction by fragmentation was not observed.

The Lago La Cocha locality (Nariño, Colombia) was more carefully studied and yielded interesting data. This is a border of tropical rain forest growing on steep slopes, with south-exposed enclaves of rockland densely covered by non-arboreal growth and cut by permanent streams whose valleys contain many logs, snags, extensive humic soils, and rotten wood. The country is foggy, relatively cold, with high rates of precipitation and with a relatively short dry season.

Deposits with remains of *H. aurea* were analyzed in order to study its bio-products. This material consisted of several kilograms of a fibrous, brown, humus-detrital, loose peat-like residue which was collected from rock shelves supporting a luxuriant bryophytic growth, dominated by upwards-directed hepatics abundantly associated with robust *H. aurea*. It is a habitat very similar to that of the Tapanti locality in Costa Rica. Material screened through a dense mesh gave two fractions: 1 - humic (meso-fragments) including *H. aurea* stems (with leaf bases only) up to 40% and, 2 - a finer one with remains of Insecta, sclerotia of Fungi, various animal cuticules, flat (up to a few mm in diameter) and spiral Gastropoda, and many

undetermined plant fragments associated with sand grains and clay.

Volcanic effects were observed on the islands of St. Vincent and Martinique. They have essential significance to the ecology and the altitudinal range of the species. After the eruption in 1979, St. Vincent I. was covered by a heavy ash fall, and in some places the resulting ash deposits were up to 1 m thick. At higher elevations branches and trunks were decorticated and erosion caused large moss-free areas. However, at lower elevations epiphytes, including *H. aurea*, were only slightly destroyed and survived this catastrophe rather better than other plants.

At upper elevations on Martinique, a fire in 1902 burnt forests and produced a considerably thick charcoal layer on which the species was not detected until recently, indicating that charcoal is not a suitable substrate for *H. aurea*.

Hurricanes, these secular factors of the Caribbean area, are able to deforest the summits of hills and accumulate enormous amounts of logs and brush in the valleys, often together with epiphytes. The stormy rains which usually follow hurricanes can also destroy epiphytic growth. However, after these catastrophes, there are more suitable habitats available for *H. aurea* than before. This fact explains why on the island of Dominica this moss is so frequent and occurs in some unexpected environments, e.g., on low shrubs among meadows or on fences. The hurricane in 1979 which caused an ecological disaster on Dominica was so powerful that things such as twigs, brush and people's personal items were blown to adjacent islands (also to Barbados). Certainly mosses were also dispersed. This evidence evokes amazement as to why this factor has not increased the occurrence of *H. aurea* over the islands of the northern Caribbean area.

Taxonomic considerations

Hemiragis aurea in the nineteenth century was variously affiliated with very different genera such as *Dicranum*, *Harpophyllum*, *Hookeria*, *Hypnum*, *Leskea* and *Mnium*. The monospecific status of the genus has been established by Britton (1914), Crum & Steere (1957), Welch (1971) and Wijk et al. (1962); see also literature cited therein. The family affiliation of *H. aurea* still is uncertain, depending on the taxonomic concepts of the Hookeriales, which now are many (see Buck 1987, 1988; Buck & Vitt 1986; Crosby 1974; Hedenäs 1996a,b; Robinson 1971, 1986; Tan & Robinson 1990; Welch 1976; and others). In this paper, the narrowest proposals of the affiliation of the species to higher taxonomic units are accepted. Crosby (1974) divided Hookeriaceae into 8 (plus *genera incerta sedis*) groups of which the Hemiragoid group consists of: *Hemiragis*, *Philophyllum*, *Rhynchostegiopsis*, *Dimorphocladon* and *Sauloma*. Even in such a narrow sense *H. aurea* anatomically and morphologically stands out from the other above-mentioned genera. Miller (1971) also proposed a narrow concept, including *H. aurea* with the Pilotrichaceae of the suborder Hookeriineae (one of three in the Hookeriales) comprising 15 genera needing a further subdivision into generic groups. Accepting the subdivision of the Hookeriaceae into groups, in the writer's opinion, *H. aurea* should form a group by itself or be treated as a separate subfamily in the traditional sense because it has no close relatives, its anatomy and morphology being very specific and primitive.

Varieties or genetic forms of *H. aurea* have not been discovered. Environmental and habit forms are indistinct and are represented by morphoses with a pendulous tendency occurring in optimal conditions of its epiphyllitic niche (see ecologics discussed above) and luxuriant upwards-growing, usually compacted stems in the terrestrial niche.

I did not find portrayed in the literature the anatomy of the costa, leaf blade and stem cross-sections of *H. aurea*, therefore they are presented here in Fig. 2. For drawings of other diagnostic features see the masterful illustrations in Sullivant & Lesquereux (1878), and also Bartram (1949), Crum (1994) and Florschütz de Waard (1986).

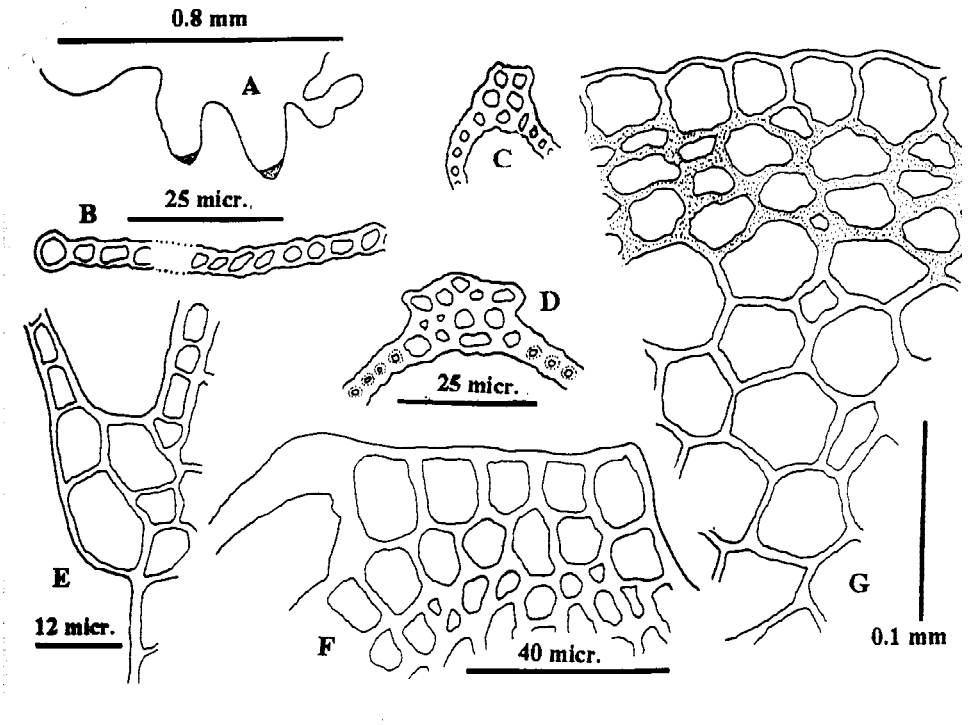

Fig. 2. Little known anatomical features of *Hemiragis aurea*: A. leaf cross-section at base. B. leaf margin and blade in cross-section. C - D. cross-sections of costa. E- F. cross-sections of leaf base. G. stem in cross-section.

Discussion

The contemporary range of *Hemiragis aurea* covers areas of a very different geologic provenance. South America belonged to Gondwanaland, the Central American isthmus was a part of the SW. fringe of Laurasia, and the islands of the Caribbean region form a specific region of their own due to their long geological history of great stresses from major geological factors such as land uplift, vulcanism, hurricanes, Atlantic and Pacific influences, a meteorite impact and many related phenomena (Benton & Little 1994, Briggs 1987, de Wit et al. 1988, Graham 1972, 1989, Kummel 1961, Raven & Axelrod 1975, Stehli & Webb 1985, Sullivan 1974, and many others).

The Central American isthmus is documented in paleogeographic and geological treatments from the Permian to Triassic periods (see, e.g., Sullivan 1974, p. 205). *Hemiragis*, however, does not occur on its oldest part (not considering its dubious locality in Guatemala), instead it is frequent in the southern part which in the middle Mesozoic to mid-Cenozoic had an insular character (Bussing 1976, Briggs 1987, Graham 1972, Sullivan 1974, and others). Once the isthmus reached South America (Stehli & Webb 1985) its old land fragments framed Atlantic and Pacific coasts on which appeared *H. aurea* in abundance. On these facts is based a suggestion that *H. aurea* in the Costa Rica-Panama region (as palaeographers call this area) has its older distribution centre inland and in the mountains, and a younger one along coasts and on lowland. Dr. B. Allen conducted an exhaustive bryological study in Honduras and did not find this moss there (pers. comm.). This seems to indicate that

the northernmost extension of this species is in northern Nicarauga.

The distribution of *Hemiragis* in northern South America is fascinating. It occurs commonly on old (often table-like) mountains in the Guiana Highlands which are based on a Precambrian bedrock plateau and have been greatly modified by various factors in the post-Cambrian eras (Briggs 1987). This portion seems to be the oldest part of the range of *Hemiragis*. The occurrence of *Hemiragis* in the Andes [Colombia to Ecuador (Bolivia?)] is strictly connected with their origin in the Tertiary, more precisely with the Tertiary uplift, and Pleistocene glaciations and deglaciations (Bürgl 1961). It is quite possible that this moss has migrated southward along deglaciated terrains.

Most enigmatic is the circum-Caribbean range of *Hemiragis*. Several speculations can be applied as an explanation of its appearance in this region, such as the meteorite impact, volcanic activities, post-volcanic changes of land and new habitat/substrate evidence, stability/ instability of islands. However, it is too difficult at the present level of bryological knowledge to decide which of these factors were directly connected with the expansion and establishment of mosses, in particular *H. aurea*.

A surprising phenomenon is the absence of this species in and around the northern Caribbean, where the bryological history is almost 250 years old. Many bryologists and amateur botanists were engaged in collecting mosses and the amount of publications on the mosses of this region is well over a hundred. In Bartram's opinion (1949) this species is "a conspicuous moss and one that would scarcely be overlooked even by a random collector". Crum (1994) incorporated *H. aurea* into the bryo-flora of Mexico stating that it "may eventually be discovered" there. This claim would be more to the point if it extended over Cuba (certainly it does not grow on the Varadero Peninsula which I carefully checked in 1992), southern Florida and southern Bahamas.

In the recent muscological literature has appeared several publications regarding the history of the moss-flora of the Middle-America, the most notable of which are Buck (1990), Delgadillo (1992), Steere (1985). Along with the literature cited in them, they show that bryological investigations are able to support geological events with the evidence provided by their fossils, ranges, ecological requirements and others.

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