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A Critique of the Genus *Boloria* (Nymphalidae) as Represented in "The Butterflies of North America", with Corrections, Additions and a Key to Species

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"The butterflies of North America" (Howe, 1975) has been criticized for a number of serious problems and errors (Belicek, 1976; Ferris, 1976; Leuschner, 1975; Orsack, 1975). Many of the generally unsatisfactory aspects are reflected in the treatment of the genus *Boloria* Moore, 1900, but there are a number of other errors that are not related to these features. It is the purpose of this paper to outline these errors and provide a basis for correcting them.

Although Howe should be commended for the quality of his illustrations (as paintings), many do not represent accurately the specimens of *Boloria*, either because of misrepresentation or transposition of plate captions. Part of this problem may be due to inaccurate reproduction of Howe's plates by the publisher. It is also unfortunate that size scales are not shown on the plates. This causes problems where size is a major distinctive character.

The author of the *Boloria* section (pages 243-252 in Howe, 1975) was Jon Shepard. He did not choose the specimens for representation, and was not asked to comment on the finished plates (Shepard, *in litt*).

Shepard also did not have an opportunity to review final page proofs, and much of his original manuscript was altered. It was first submitted in 1968, and a new one was submitted at a later date. Descriptions of species or subspecies appearing after 1968 were added by the reviewing editor, Dr. A. B. Klots. Some subspecies descriptions which appeared too late for inclusion are added herein.

Errors, Omissions, and their Corrections

1. Size of Figures.

It was mentioned earlier that size scales were not included with the plates. Presumably this is because *Boloria* figures were reported to be reproduced at actual size (Howe, 1975: 306, facing page). This is not correct. Plates of Lycaenidae were also produced at life size, but in comparing sections of these two groups of plates, our largest *Boloria*

species appear little larger than many of the average sized Lycaenidae. It appears that some of the Lycaenidae are reproduced slightly larger and the *Boloria* slightly smaller than actual size.

2. Keys.

No key to the species of the genus *Boloria* was provided. Because a good key is almost indispensable to a collector who is unfamiliar with a group of species, I have constructed a simple key to the genus *Boloria* in North America. It is designed for field use without dissections or the use of visual aids, so certain diagnostic characters that are normally concealed from the eye are not used. The key is not sufficiently detailed to make possible identification of aberrant specimens, intergrades, or specimens at the extremes of normal variation in certain species.

The species of the genus *Boloria* are arranged in three subgenera: *Clossiana, Proclossiana, and Boloria.* Because the last two subgenera contain only one species each in North America, *B. eunomia* and *B. napaea* respectively, a key to subgenera is not provided.

The key was constructed from the study of specimens in my collection, and from original descriptions of the taxa in question.

Key to Adults of the Species of Boloria in North America

Abbreviations: VFW - Ventral fore wing VHW - Ventral hind wing FW - Fore wing

1a. Submarginal spots of VFW whitish or silvered..... 2

b. Submarginal spots of VFW not whitish or silvered..... 12 2a(1a). Spots in postmedian-submarginal area of VHW open and silver or yellow centered..... eunomia (Esper, 1799)

b. Spots in postmedian-submarginal area of VHW closed, not silvered or yellow..... 3

3a(2b). Submarginal spots of VFW silvered or white (NOTE: some specimens of *B. selene tollandenis* have silvering reduced, but not absent)..... 4

b. Submarginal spots of VFW not silvered or white..... 6
4a(3a). Submarginal spots of VHW extended to and disrupting margin of wing..... 5

b. Submarginal spots of VHW not as above..... selene (Denis and Schiffermueller, 1775)

5a(4a). At least some submarginal spots of VHW capped by dark triangles with bases of some bent markedly basad (Fig.2)..... freija (Thunberg, 1791)

b. All submarginal spots of VHW capped by dark triangles with bases unbent, or only slightly bent basad (Fig. 3).... polaris (Boisduval, 1828)

6a(3b). Submedian-median band of VHW continuous, solidly white, and bordered by heavy black..... astarte (Doubleday, 1847)

b. Submedian-median band of VHW broken or solid, but if solid, then tinted with yellow or brown..... 7

7a(6b). Portion of submedian-median band of VHW in discal cell silvered, the remainder unsilvered..... napaea (Hoffmansegg, 1804)
b. Not as above..... 8

8a(7b). Submedian-median band of VHW continuous and solidly yellow (in part; see note on page)..... titania (Esper, 1793)

b. Submedian-median band of VHW broken, or not solidly yellow
 9

9a(8b). Submedian-median band of VHW clearly edged in black 10

b. Submedian-median band of VHW not edged in heavy black (see note on page)..... chariclea (Schneider, 1794)

10a(9a). Apical portion of VFW distinctly darker than rest of wing 11

b. Apical portion of VFW not distinctly darker than rest of wing distincta (Gibson, 1920)

11a(10a). Postmedian band of VHW represented by a continuous band of white (in part)..... freija (Thunberg, 1791)

b. Postmedian band of VHW incomplete or if complete, only costal portion clearly white (in part; see note on page)..... titania (Esper, 1793)

12a(1b). Apical margin of FW angled; not smoothly curved (NOTE: some specimens of *B. bellona* from Alberta and British Columbia have this angle reduced and will key out to *frigga*. These can be distinguished from specimens of *frigga* by their brighter ground color on the VFW.)..... ... bellona (Fabricius, 1775)

b. Apical margin of FW evenly curved..... 13
13a(12b). Submedian-median band of VHW between Sc and Rs distinctly lighter than majority of remaining band..... 16

b. Submedian-median band of VHW uniformly colored..... 14 14a(13b). Submedian-median band of VHW in sharp contrast with rest of wing..... kriemhild (Strecker, 1878)

b. Submedian-median band of VHW not in sharp contrast with rest of wing..... 15

15a(14b). Black markings on VFW sharp and distinct (in part)...... ... epithore (Edwards, 1864)

b. Black markings on VFW weak and indistinct; rarely one or two sharp and distinct..... *alberta* (Edwards, 1890)

16a(13a). Markings on VFW weak; no distinct black spots.... improba (Butler, 1877)

Markings on VFW strong; Black spots distinct..... b. 17 17a(16b). Base of VHW at junction of Sc and R-M with silver spot (Fig. 4)

frigga (Thunberg, 1791)

Base of VHW at junction of Sc and R-M lacking silver spot (in part: b. NOTE: specimens of frigga from the Dempster Highway, Yukon, tend to have this spot reduced or lacking, and also lack the darker coloration of frigga. These can be separated from specimens of epithore by indistinct markings on the VFW..... epithore (Edwards, 1864)

NOTE: One of the major identification problems in this genus is distinguishing between B. titania and B. chariclea. These taxa intergrade in the Yukon and NWT, and Dr. C. D. Ferris has mentioned similar zones of possible intergradation in Alaska, northern Manitoba, and Labrador. Some specimens from Wyoming and Colorado, U.S.A., key out to B. chariclea. Before 1950 the forms now considered subspecies of B. titania were treated as forms of B. chariclea, or as separate species. Between 1950 and 1953 most of these subspecies were transferred to B. titania (Klots, 1951a, 1951b, 1953) without publication of the reasoning behind this decision. Recent work (Pike, in prep.) indicates that all North American subspecies are more similar to B. chariclea than to B. titania. It is outside the scope of this paper to present the reasons for this. For the sake of consistency with the presentation in Howe (1975), I follow Klots, bearing in mind that the Klots system is probably not the most accurate for presentation of the relationship between taxa.

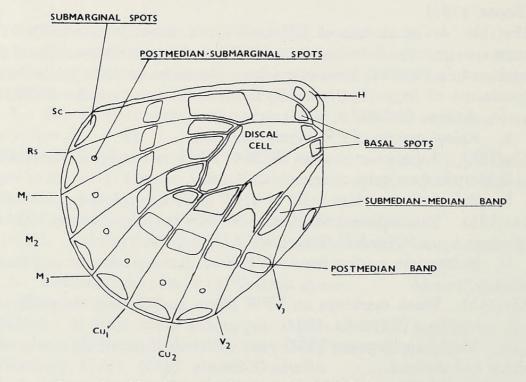


Fig. 1. Generalized hind wing of the genus Boloria showing important veins and markings on ventral surface: H, humeral vein; Sc, subcosta; Rs, radial sector; M, median; Cu, cubitus; V, vannus, or anal veins.

3. Author of the generic name Boloria

The generic name Boloria is credited to Reuss (Shephard, in Howe, 1975, page 243). In fact, it was proposed by Moore in 1900, the type species being *Papilio pales* Denis and Schiffermueller, 1775. In Europe it is restricted to the *pales-napaea-graeca* group of species, presumably first by Reuss, and later by Warren (1944).

4. Boloria napaea reiffi Reuss, 1925

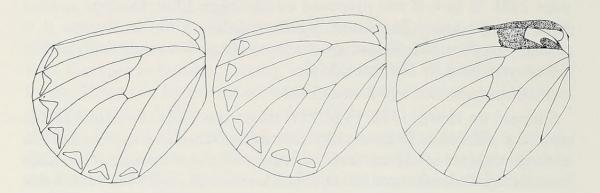
Shepard (in Howe, 1975, page 244) treats this form as consubspecific with B. n. alaskensis Holland, 1900. It was described as a species and has been the subject of controversy ever since. The type specimen is a male from British Columbia and has not been located. Klots (1940) treated this taxon as a subspecies and suggested it may be consubspecific with B. n. alaskensis. He had not seen the type but had located a specimen from Atlin, British Columbia, with characters resembling those of the description of B. reiffi. Warren (1944) also treated it as a subspecies, mentioned Klots' suggestion, and added one of his own; "The locality suggests that it might be a slightly abnormal specimen of subspecies alaskensis." He had not seen material of either B. reiffi or B. n. alaskensis. Dos Passos (1964) listed it as a subspecies as well. Shepard has synonymized the names B. reiffi and B. n. alaskensis, following the opinions of Klots and Warren. However, there is no justification for changing the status of B. reiffi now. A decision about its status must be based on study of the holotype or material that shares characteristics of this specimen. Possibly, such material is represented by unstudied specimens from colonies of Boloria near Fort Saint John, British Columbia, and north of Hinton, Alberta. Presumably it is considered a subspecies of B. napaea from characters given in the description and because of the lack of knowledge and specimens referable to this taxon.

5. Boloria eunomia (Esper, 1799)

Shepard (in Howe, 1975, page 245) has misidentified Boloria eunomia nichollae (Barnes and Benjamin, 1926). There are two forms of B. eunomia found in the Rocky Mountains of Alberta and British Columbia; a light one and a dark one. Shepard has applied the name to the light form generally distributed in the Rocky Mountains, where, in fact, it should be restricted to the dark form found only in the vincinity of the Columbia Ice Fields, Alberta. From the original description, reproduced below, it is obvious that the specimen figured as B. e. nichollae (Howe, plate 34, Fig. 3) is not properly assigned.

"Upper side similar to dark specimens of *dawsoni*. Under side similar to *dawsoni* but darker, especially on the hind wing. We suspect this is a high altitude form."

Specimens of *B. e. nichollae* are stated by the authors to be darker on the underside than specimens of *B. e. dawsoni*. This is not true of the figured



- Fig. 2. Ventral Hind Wing of *Boloria freija* showing triangular caps on spots of submarginal band. Note the angled bases.
- Fig. 3. Ventral Hind Wing of *Boloria polaris* showing triangular caps on spots of the submarginal band. Note the relatively straight bases.
- Fig. 4. Ventral Hind Wing of *Boloria frigga* showing average extent of silvering in the area of the junction of Sc and R-M.

specimen. Ferris (1971) states that B. e. nichollae is a melanic high altitude form. The specimen figured is not melanic.

Shepard's justification for considering *B. e. nichollae* to be the light form generally distributed in the Canadian Rocky Mountains is that the collector, a Mrs. Nicholls, did not get closer to the Columbia Ice Fields than Laggan, Alberta, on her 1904 trip (Shepard, *in litt.*). Mrs. Nicholls (1905) published the itinerary of her trip, and from the dates and localities mentioned, she could not have visited the Ice Fields area. Subsequently, however, she collected specimens of *B. alberta* and *B. astarte* at the headwaters of the Saskatchewan and Athabasca rivers (Entomogical Society of Ontario, season summary page 118, 1907). These rivers emanate from the Columbia Ice Fields. At the same time, she probably collected the specimens that were eventually named *B. e. nichollae*. Examination of one male paratype from the USNM supports this hypothesis. Figure 5 illustrates the differences between *B. e. nichollae* and *B. e. dawsoni* from Alberta.

There has been some confusion about the type locality of *B. e. triclaris*. Shepard (page 245) states that the type locality is Labrador. Holland (1928) wrote that the type locality was "undoubtably Labrador". Barnes and Benjamin (1926) state that a short series of Labrador specimens is not similar in color pattern to specimens figured in Huebner's plates. Ferris

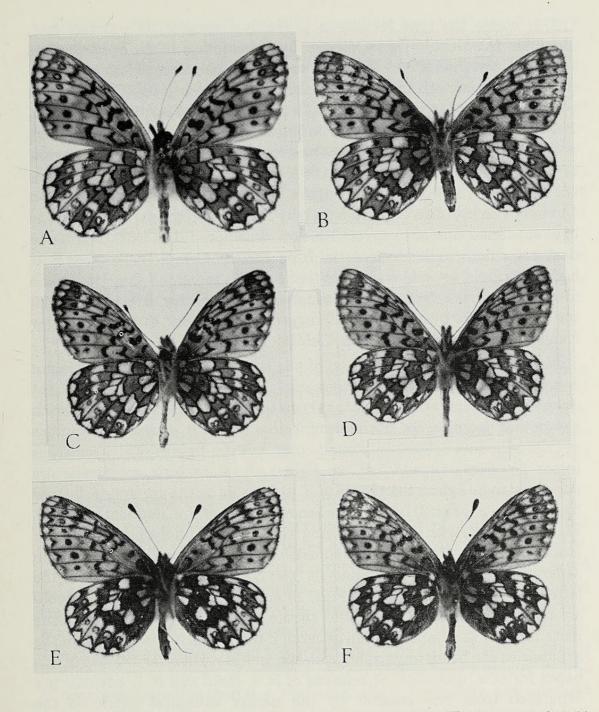


Fig. 5A. Boloria eunomia dawsoni male, Beaver Flats, Alberta, 18 VI 1971, Ted

- Fig. 5B. Boloria eunomia dawsoni female, Plateau Mt., Alberta, 7500', 26 VII 1975, Ted Pike
- Fig. 5C. Boloria eunomia dawsoni male, 7 mi. E. Athabasca, Alberta, 16 VI 1974, Ted Pike
- Fig. 5D. Boloria eunomia dawsoni male, 50 mi. W. Edmonton, Alberta, 18 VI 1976, Ted Pike
- Fig. 5E. Boloria eunomia nichollae male, Wilcox Pass, Alberta, 7 VIII 1976, Ted Pike
- Fig. 5F. Boloria eunomia nichollae male, Wilcox Pass, Alberta, 7 VIII 1976, Ted Pike

(1971) states the type locality is probably Labrador. In point of fact, Huebner fixed the type locality in his description of B. e. triclaris as Labrador, but the Labrador of 1821 was not the Labrador of today. Figures 6 and 7 show two official views of Labrador in the early 1800's, and much confusion existed at the time both officially and for the layman (Nicholson, 1954). Holland (1928) states that he had available specimens from eastern and western Labrador "that is, the eastern shore of Hudsons Bay." In view of this, I suggest that Huebner's concept of Labrador could have encompassed the whole of the Ungava Penninsula north of what was then Quebec. The problem is complicated by Huebner's figures. He shows one light specimen similar to specimens now considered B. e. triclaris and one dark specimen similar to material from Baker Lake, N.W.T., or to B. e. nichollae. Field (in litt.) and Klots (in litt.) have indicated that Huebner's material has been destroyed. Because B. e. triclaris has been considered the light form for over 150 years, I suggest it be retained as such. The type locality is nereby fixed as Nain, Labrador, Canada.

Unfortunately, characterization of the subspecies of B. eunomia is not complete (plate 245). B. e. dawsoni, caelestis, and nichollae are not described. Presumably we are to rely on the plates, but close examination shows that these do not fit the descriptions given. B. e. denali specimens are described as lightest in ground color, but the figures of B. e. caelestis (plate 35, Figs. 13 and 14) are lighter. B. e. triclaris specimens are supposed to be lighter than those of B. e. dawsoni on the upperside, but the figure (plate 34, Fig. 2) is much the same as those of B. e. dawsoni (plate 35, Figs. 16 and 17) with the latter having a lighter band on the hind wing. B. e. laddi specimens are stated to be unsilvered, this character to be used in separating them from, specimens of B. e. caelestis, but the figures of the latter are unsilvered (plate 34, Figs. 13 and 14). Specimens of B. e. laddi are not figured. All the subspecies should have been figured on the same plate for ease of comparison. In general, if the text is followed most of the subspecies can be distinguished from one another, but refer to Fig. 5 of this paper for B. e. nichollae. Specimens of B. e. laddi and B. e. caelestis are separated from one another by the darker subapical patch on the underside of the forewing, and the darker submarginal, median, and postbasal bands on the ventral forewing on B. e. laddi (Klots, 1940). B. e. dawsoni specimens are identified by their dark ground color, bright red bands and silvered markings on the ventral hind wing.

6. Boloria selene (Denis and Schiffermuller, 1775)

The name *B. selene albequina* is considered a junior synonym of *B. selene atrocostalis* (pate 246). Kohler (1977) revised this species, and retained *B. s. albequina* as a valid subspecies.

Here, again, the text and plates do not tally. B. s. atrocostalis is claimed to be intermediate between B. s. myrina and B. s. terraenovae in color and

maculation (Shepard, in Howe, 1975, page 246) but the plates show B. s. atrocostalis (plate 34, Fig. 18) as the darkest of the three, with B. s. terraenovae (plate 34, Fig. 9) between it and B. s. myrina (plate 35, Fig. 1). Specimens of B. s. nebraskensis are distinguished from those of B. s. myrina by their larger size, but the figures are much the same and there are no scales to indicate size. Shepard states that six subspecies were described from North America but considers only five. Presumably B. s. albequina is to be the sixth, but what, then, of B. s. marilandica (Clark, 1941)? Both were subspecies described from North America, which makes a total of seven, two of which are not considered valid. Kohler (1977) has added an eighth subspecies, B. s. sabulocollis.

If the text is followed, the five subspecies are distinguishable from each other using the figure of *B. s. myrina* as a reference. *B. s. sabulocollis* is distingushed by its greater amount of yellow dusting on the VHW than *B. s. myrina*.

7. Boloria bellona (Fabricius, 1775)

The illustrations (plate 35, Figs. 4, 5 and 6) do not fit the descriptions in the text. B. bellona toddi specimens are stated to have the basal portion of the upperside of the wings dark, and specimens of B. b. bellona are stated to lack this darkening. Specimens of B. b. jenistai are said to have less darkening than B. b. toddi but more than specimens of B. b. bellona (page 247). The figures are much the same. Again the text is reliable.

8. Boloria epithore (Edwards, 1864)

Perkins and Perkins (1973) revised this species and treated four subspecies. The two new subspecies are *B. e. borealis* and *B. e. sierra*. Although there has been some controversy over the validity of these subspecies (Shepard, *in litt.*; Parshall, *in litt.*), until something is published refuting this work, these subspecies should be considered valid. Unfortunately, *B. e. borealis* is a junior homonym of *B. thore borealis* (Staudinger, 1861). Steps are being taken to correct this. The four subspecies can be distinguished as follows: *B. e. "borealis"* specimens have a greater degree of basal black dusting than *B. e. chermocki* and *B. e. epithore*, and they also have greyish marginal markings on the dorsal surface; specimens of *B. e. sierra* are distinguished by their greater degree of ferruginous coloring on the ventral surface.

9. Boloria kriemhild (Strecker, 1878)

Because adults of *B. kriemhild* and *B. epithore* are markedly similar in external features, illustrations of the two should appear on the same plate, for ease of comparison. Instead *B. epithore* is figured on plate 34, *B. kriemhild* on plate 33.

10. Boloria frigga (Thunberg, 1791)

Details in the description of B. f. sagata do not fit the specimen figured (plate 33, Fig. 4). Specimens are stated to have a lighter upperside than

those of the other subspecies (plate 248), but on the plates they are the same. A series of 16 specimens from Colorado shows the upperside to be lighter than Alberta or Yukon material (excluding Dempster Highway, Yukon, material). Specimens of *B. f. saga* are supposed to have the basal area on the upperside suffused with black, but the plates show all subspecies with similar suffusion. The text is reliable.

The status of the Dempster Highway material is as yet unknown.

11. Boloria titania (Esper, 1793)

The six subspecies are not characterized in the text (pate 250). Rather than rely on the plates, I have prepared brief characterizations from the original descriptions. B. t. boisduval - median 0 submedian band not solidly white or yellow. Underside suffused with deep purple. Average

B. t. boisduvali - median 0 submedian band not solidly white or yellow. Underide suffused with deep purple. Average wingspan, 35 mm.

B. t. grandis - coloration as per B. t. boisduvali. Underside suffused with purple, and darker. Average wingspan, 40 mm.

B. t. montinus - median-submedian bank largely lacking white or yellow scaling. Underside without purple suffusion, tending to be more red. Less contrast on ventral hind wings.

B. t. rainieri - median-submedian band more yellow than preceeding subspecies. Much more contrast on hind wing underside than B. t. montinus.

B. t. helena - median-submedian band almost solidly yellow. No purple suffusion, tending to red-brown.

B. t. ingens - median-submedian band almost solidly yellow. Larger and darker than B. t. helena.

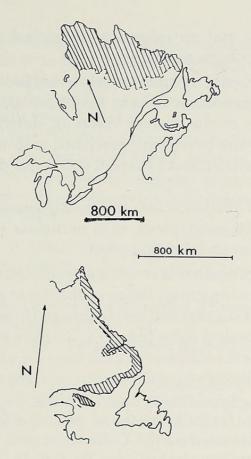
11. Boloria alberta (Edwards, 1890)

Shepard states that adults are present every year at Plateau Mt., Alberta (Shepard, in Howe, page 250). This is not quite true. It is true that they are not restricted to even-numbered years, but there are years in which no adults can be seen. It would seem, then, that adults are not present every year.

The type locality is Laggan, Alberta, the name of which was changed many years ago to Lake Louise Junction.

12. Boloria astarte (Doubleday, 1847)

Shepard considers *B. distincta* conspecific with *B. astarte* (Howe, 1975: 251). He also states that there is some controversy over this opinion. If this is so, it is best to leave *B. distincta* as the author described it, as a species, until its status is elucidated by study. The alternative is to change its status without adequate justification.



- Fig. 6. Labrador according to the Hudsons Bay Company map by J. Arrowsmith published 1832. From "The Boundaries of Canada, its Provinces and Territories" by N. L. Nicholson.
- Fig. 7. The limits of Labrador according to the Labrador act, 1809. From "The Boundaries of Canada, its Provinces and Territories" by N. L. Nicholson.

13. Boloria polaris (Boisduval, 1828)

If two subspecies are recognized, the figures (plate 34, Figs. 16 and 17) should be designated as one of these two subspecies and not simply B. *polaris*. Fortunately, adequate characterization is given in the text.

B. p. gorenlandica is omitted, presumably because it was described from Greenland, but specimens from Devon Island, N.W.T., agree with figures of B. p. groenlandica. If this subspecies is considered to be consubspecific with B. p. polaris, this should be mentioned in the text.

Discussion

In conclusion, the treatment of questionable or little known taxa is inconsistent. The name *B. reiffi* is relegated to synonymy, but the names *B. freija natazati* (Gibson, 1920) and *B. freija nabokovi* (Stallings and Turner, 1946) are considered valid, even though Shepard admits that he knows nothing more of these forms than is contained in the type descriptions, which is equal to his knowledge of *B. reiffi*. There is no discussion of taxonomic changes and no reference to original work in which these changes might have been published.

There is no discussion of where work is needed in this genus. In my opinion, the most important tasks in the future are:

1. Determination of the correct status of described forms in North America. Some of the previously described taxa were based on inadequately studied material, and I suspect that many do not represent valid taxa.

2. Elucidation of relationships, and construction of phylogenies, and reconstruction of biogeographies, with particular reference to relationships with European and Asian species.

In view of the large number of errors and inconsistencies in the treatment of this rather well known genus, I imagine that other genera will also be in a similar state. If so, I suggest that corrections to Howe's book be published or deposited in a central collecting area, perhaps with the publishers or with the editor. These could serve as the basis for a revised and corrected volume, should author and publisher care to issue a new edition.

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