Notes on the *Lethe latiaris* (HEWITSON, 1863)-complex with the descriptions of new taxa from S.W. China

(Lepidoptera, Nymphalidae, Satyrinae)

by

Song-Yun Lang received 9.V.2020

Abstract: In this paper, the *Lethe latiaris* (HEWITSON, 1863)-complex is studied. As a result, the following new species and subspecies are described from S.W. China. They are *Lethe eitschbergeri* spec. nov. from S.E. Yunnan and W. Guangxi, *L. eitschbergeri* zhujqi subspec. nov. from N.W. Yunnan, and *L. latiaris cenwanga* subspec. nov. from W. Guangxi. *Lethe unistigma* LEE, 1985 is sunk to a subspecies of *L. latiaris* (HEWITSON), viz. *L. latiaris unistigma* LEE stat. nov.

The Lethe latiaris (HEWITSON, 1863)-complex belongs to the minerva (FABRICIUS, 1775)-group (DE LESSE, 1957) of the subgenus Lethe HÜBNER, [1819] (Satyrini: Lethina). Until now, 4 species of the complex have been recognised, they are *L. latiaris* (HEWITSON) from the south slope of C. & E. Himalayan region and N. Indo-China, *L. unistigma* LEE, 1985 from E. Yunnan and W. Guangxi, *L. guansia* SUGIYAMA, 1999 from E. Guangxi and N.W. Guangdong, and *L. konkakini* MONASTYRSKII & DEVYATKIN, 2000 from C. Vietnam (MONASTYRSKII, 2005; LANG, 2017). Among them, *Lethe latiaris* (HEW.) has 4 subspecies, viz. the nominate subspecies from E. Himalayan region (S.E. Tibet, Bhutan, N.E. India, N. Myanmar), subspec. *hige* FUJIOKA, 1970 from C. Himalayan region (Nepal), subspec. *perimele* FRUHSTORFER, 1911 from N. Indo-China (W. & S. Yunnan, Vietnam, Laos, E. Myanmar, N. Thailand), and subspec. *lishadii* HUANG, 2002 from N.W. Yunnan (Nujiang valley) (LANG, 2017). In this paper; a new species and two new subspecies from S.W. China (Yunnan and W. Guangxi) are described. Moreover, *Lethe unistigma* LEE, 1985 is sunk to a subspecies of *L. latiaris* (HEWITSON). Specimens in this study are kept in Chongqing Museum of Natural History, Chongqing, CHINA (CMNH); Institute of Zoology, Chinese Academy of Sciences, Beijing, CHINA (IZCAS); SONG-YUN LANG's private collection, Shuangliu, Chengdu, CHINA (LSY).

Lethe eitschbergerispec. nov. (Figs. 11-14, 18)

HT (Holotype) J, CHINA, Yunnan, Pingbian, Dawei-shan, 2000 m, 2.V.2019, leg. S-Y. LANG, CMNH.

PT (Paratypes): 1 °, same data as HT, LSY; 1 °, 1 °, CHINA, Yunnan, Xichou, Jiguan-shan, 1700 m, 30.IV.2019, leg. S-Y. LANG, LSY; 1 °, CHINA, Yunnan, Malipo, Laoshan Reserve, 1580 m, 29.IV.2019, leg. YI LANG, LSY; 5 °°, CHINA, Guangxi, Tianlin, Mt. Cenwang-laoshan, 1300-1700 m, 6.-10.V.2015, leg. S-Y. LANG, LSY.

Notes: The new species flies together with *Lethe latiaris* (HEW.) in S.E. Yunnan and W. Guangxi, $\sigma\sigma$ of these two sympatric species are very similar but can be separated from each other by some very stable differences, and, furthermore, their \mathfrak{P} are quite different. The new species is similar and very closely related to *L. konkakini* MONAST. & DEVY. from C. Vietnam. At first, I thought it should be a subspecies of *L. konkakini* MONAST. & DEVY., but here I still described it as a distinct species basing upon differences in σ genitalia and φ external appearance. Of course, material of *L. konkakini* MONAST. & DEVY. has not been studied by myself and information of its features is known from literatures (MONASTYRSKII & DEVYATKIN, 2000; MONASTYRSKII, 2005). Therefore, some details of σ genitalia and androconia of *L. konkakini* MONAST. & DEVY. cannot be examined. Moreover, differences between the new species and *L. guansia* SUGIYAMA, 1999 are obvious, so it doesn't need a further discussion.

Diagnosis: A) The new species can be easily distinguished from *L. latiaris* (HEW.) by the combination of the following characters: a1) on \circ underside, forewing postdiscal line is very close to the lower angle of the cell in the new species, whereas it is far beyond the lower angle in *L. latiaris* (HEW.); a2) on both sides of \circ , white forewing postdiscal band is very broad in the new species, whereas it is very thin in *L. latiaris* (HEW.); a3) androconia of the new species (Fig. 20: f1-4) are obviously shorter that those of *L. latiaris* (HEW.) (Fig. 20: b, c, d1-5, e1-2); a4) the uncus of the new species (Fig. 22: b) is very strongly dorsally swollen, whereas it is only weakly swollen in *L. latiaris* (HEW.) (Fig. 22: d); a5) the valva apex is somewhat pointed in the new species (Fig. 24: a1-4), whereas it is nearly rounded in *L. latiaris* (HEW.) (Fig. 24: c, d, e1-2, f1-2); a6) the caudal crest of the aedoeagus is more expanded outwards in the new species (Fig. 23: a1-3), whereas it is obviously less expanded in *L. latiaris* (HEW.) (Fig. 23: b1-6).

B) The new species can be distinguished from *L. konkakini* MONAST. & DEVY. by the combination of the following characters: b1) the uncus of the new species (Fig. 22: b) is very strongly dorsally swollen and its crest is somewhat nearer to the apex, whereas it is comparatively weakly dorsally swollen and its crest is near the middle in *L. konkakini* MONAST. & DEVY. (Fig. 22: c); b2) on upperside, \Im forewing white postdiscal band is bent downwards near the tornus and touching the vein 1b in the new species, whereas it is not bent downwards and far away from the vein 1b in *L. konkakini* MONAST. & DEVY.; b3) on underside, \Im forewing distal half and hindwing submarginal area are yellowish brown in the new species, whereas they are deep and reddish brown in *L. konkakini* MONAST. & DEVY. Etymology: The specific name *eitschbergeri* is named after the chairman and editor of Atalanta, Dr. ULF EITSCHBERGER (Marktleuthen). Distribution: China (S.E. Yunnan, W. Guangxi), ?N. Vietnam.

Lethe eitschbergeri z h u j q i subspec. nov. (Figs. 15)

HT J, CHINA, Yunnan, Gongshan, Dulongjiang, Bapo, 1500 m, 31.V.2009, leg. JIANQING ZHU, CMNH.

Diagnosis: The new subspecies from N.W. Yunnan can be distinguished from the nominate subspecies from S.E. Yunnan and W. Guangxi by the combination of the following characters: 1) the new subspecies is smaller than the nominate subspecies; 2) uncus of the new subspecies (Fig. 22: a) is more stubby than that of the nominate subspecies (Fig. 22: b); 3) valva apex of the new subspecies (Fig. 24: b) is sharply pointed, whereas it is weakly pointed in the nominate subspecies (Fig. 24: a1-4).

Etymology: The subspecific name *zhujqi* is named after Mr. ZHU JIANGQING (Shanghai). Distribution: China (N.W. Yunnan), ?N. Myanmar.

Lethe latiaris unistigma LEE, 1985 stat. nov. (Fig. 7)

Lethe unistigma LEE, 1985, Entomotaxonomia 7 (3): 193. TL: Shi-zong, Yunnan.

Material: HT J, CHINA, Yunnan, Shi-zong, 1280 m, 1979-IV-20, leg. YUANZHONG WANG (IZCAS).

Notes: Only the HT σ has been known, and both, its σ genitalia and androconia, are unknown. However, it is clear that its σ forewing underside postdiscal line is far beyond the lower angle of the cell, whereas in the other easily confusing species in *latiaris*-complex it is very close to the lower angle of the cell. Therefore, it should be *Lethe latiaris* (HEW.), but not a distinct species. Without additional information I cannot sunk it as a junior synonym under any known subspecies, so here it is treated as *L. latiaris unistigma* LEE, 1885 **stat. nov.**

Diagnosis: This subspecies can be distinguished from its nearby subspecies *Lethe latiaris perimele* FRUHST. by the following characters: 1) obviously smaller in size; 2) on upperside, σ hair tuft alongside vein 3 is much shorter; 3) on underside, forewing ocelli are reduced.

Distribution: China (E. Yunnan).

Lethe latiaris c e n w a n g a subspec. nov. (Figs. 8, 9)

HT J. CHINA, Guangxi, Tianlin, Mt. Cenwang-laoshan, 1400 m, 8.V.2015, leg. S-Y. LANG (CMNH). PT 7 J. Rame locality as HT 1300-1700 m, 6.-10.V.2015, leg. S-Y. LANG (LSY).

Diagnosis: In LANG (2017), the present author provisionally considered this population from W. Guangxi as *Lethe unistigma* LEE, 1985. Geographically, the range of *L. latiaris unistigma* LEE **stat. nov.** lies to the west of this population, and the range of *L. latiaris perimele* FRUHST. lies to its southwest. The new subspecies can be distinguished from them by the combination of the following characters: 1) It is larger in size than *L. latiaris unistigma* LEE **stat. nov.**; 2) on upperside, σ hair tuft alongside vein 3 is much longer than that of *L. latiaris unistigma* LEE **stat. nov.**; 3) on underside, its ground colour is more yellowish than those of *L. latiaris unistigma* LEE **stat. nov.**; 4) on forewing underside, no purple line is present in discal area, whereas in *L. latiaris perimele* FRUHST. it is more or less present alongside the outer edge of the ochreous postdiscal line. Etymology: The subspecific name *cenwanga* is named after Mt. Cen-wang, the type locality.

Distribution: China (W. Guangxi).

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Fig. 1: Lethe guansia SUGIYAMA, 1999, J, Guangxi, Jinxiu, LSY. Fig. 2: Lethe latiaris (HEW., 1863), J, Tibet, Zayu, SATY0484, ANDR0162, LSY. Fig. 3-6: Lethe latiaris perimele FRUHST., 1911: (3) J, Yunnan, Ximeng, ANDR0164, LSY; (4) ditto, Yingjiang, SATY0825, ANDR0157, LSY; (5) ditto, Xichou, SATY0831, ANDR0173, LSY; (6) ditto, Xichou, ANDR0158, LSY. Fig. 7: Lethe latiaris unistigma LEE, 1985 stat. nov., HT J, Yunnan, Shizong, IZCAS. Fig. 8-9: Lethe latiaris cenwanga subspec. nov.: (8) HT J, Guangxi, Tianlin, SATY0362, ANDR0159, CMNH; (9) PT, ditto, SATY0832, ANDR0160, LSY. Fig. 10: Lethe konkakini MoNAST. & DEVY., 2000, J, C. Vietnam, after MONASTYRSKII & DEVYATKIN (2000). Fig. 11-14: Lethe eitschbergeri spec. nov.: (11) PT J, Guangxi, Tianlin, SATY0828, ANDR0170, LSY; (12) HT J, Yunnan, Pingbian, SATY0826, ANDR0165, CMNH; (13) PT, ditto, Xichou, SATY0830, ANDR0172, LSY; (14) ditto, Malipo, SATY0827, ANDR0167, LSY. Fig. 15: Lethe eitschbergeri zhujqi subspec. nov., HT J, Yunnan, Dulongjiang, SATY0829, ANDR0163, CMNH.



Fig. 16: *Lethe latiaris lishadii* HUANG, 2002, ♀, Yunnan, Gongshan, LSY. Fig. 17: *Lethe guansia* SUGIYAMA, 1999, ♀, Guangdong, Ruyuan, LSY. Fig. 18: *Lethe eitschbergeri* spec. nov., PT ♀, Yunnan, Xichou, LSY. Fig. 19: *Lethe konkakini* MONAST. & DEVY., 2000, ♀, C. Vietnam, after MONASTYRSKII & DEVYATKIN (2000).



Fig. 20: Androconia. (a) Lethe guansia SUGIYAMA, 1999, Guangdong, Ruyuan, ANDR0174, LSY; (b) Lethe latiaris (HEW., 1863), Tibet, Zayu, ANDR0162, LSY; (c) Lethe latiaris lishadii HUANG, 2002, Yunnan, Gongshan, ANDR0171, LSY; (d1) Lethe latiaris perimele FRUHST., 1911, Yunnan, Yingjiang, ANDR0157, LSY; (d2) ditto, Ximeng, ANDR0164, LSY; (d3) ditto, Xichou, ANDR0173, LSY; (d4) ditto, ANDR0166, LSY; (d5) ditto, ANDR0158, LSY; (e1) Lethe latiaris cenwanga subspec. nov. HT Guangxi, Tianlin, ANDR0159, CMNH; (e2) ditto, PT, ditto, ANDR0160, LSY; (f1) Lethe eitschbergeri spec. nov., PT, Guangxi, Tianlin, ANDR0170, LSY; (f2) ditto, PT, Yunnan, Xichou, ANDR0172, LSY; (f3) ditto, HT, Yunnan, Pingbian, ANDR0165, CMNH; (f4) ditto, PT, Yunnan, Malipo, ANDR0167, LSY; (g) Lethe eitschbergeri zhujqi subspec. nov., HT, Yunnan, Dulongjiang, ANDR0163, CMNH.



Fig. 21: & genitalia in lateral view with left valva and aedoeagus removed. (a) *Lethe eitschbergeri* spec. nov., HT, Yunnan, Pingbian, SATY0826, CMNH; (b) ditto, PT, Yunnan, Malipo, SATY0827, LSY; (c) ditto, PT, Yunnan, Xichou, SATY0830, LSY; (d) ditto, PT, Guangxi, Tianlin, SATY0828, LSY; (e) *Lethe eitschbergeri* zhujqi subspec. nov., HT, Yunnan, Dulongjiang, SATY0829, CMNH; (f) *Lethe konkakini* MONAST. & DEVY., 2000, C. Vietnam, after MONASTYRSKII & DEVYATKIN (2000); (g) *Lethe latiaris* (HEW., 1863), &, Tibet, Zayu, SATY0484, LSY; (h) *Lethe latiaris lishadii* HUANG, 2002, Yunnan, Gongshan, SATY0833, LSY; (i) *Lethe latiaris perimele* FRUHST., 1911, Yunnan, Xichou, SATY0831, LSY; (j) *Lethe latiaris cenwanga* subspec. nov., HT, Guangxi, Tianlin, SATY0362, CMNH; (k) ditto, PT, ditto, SATY0832, LSY; (l) *Lethe guansia* SUGIYAMA, 1999, Guangdong, Ruyuan, SATY0540, LSY.



Fig. 22: Uncus in lateral view. (a) *Lethe eitschbergeri zhujqi* subspec. nov., HT, Yunnan, Dulongjiang, SATY0829, CMNH; (b) *Lethe eitschbergeri* spec. nov., HT, Yunnan, Pingbian, SATY0826, CMNH; (c) *Lethe konkakini* MONAST. & DEVY., 2000, C. Vietnam, modified from MONASTYRSKII & DEVYATKIN (2000); (d) *Lethe latiaris perimele* FRUHST., 1911, Yunnan, Xichou, SATY0831, LSY; (e) *Lethe guansia* SUGIYAMA, 1999, Guangdong, Ruyuan, SATY0540, LSY.



Fig. 23: Aedoeagus in lateral and dorsal view. (a1) *Lethe eitschbergeri* spec. nov., holotype, Yunnan, Pingbian, SATY0826, CMNH; (a2) ditto, PT, Yunnan, Xichou, SATY0830, LSY; (a3) ditto, PT, Guangxi, Tianlin, SATY0828, LSY; (a4) *Lethe eitschbergeri zhujqi* subspec. nov., holotype, Yunnan, Dulongjiang, SATY0829, CMNH; (b1) *Lethe latiaris* (HEW., 1863), σ , Tibet, Zayu, SATY0484, LSY; (b2) *Lethe latiaris lishadii* HUANG, 2002, Yunnan, Gongshan, SATY0833, LSY; (b3) *Lethe latiaris perimele* FRUHST., 1911, Yunnan, Yingjiang, SATY0825, LSY; (b4) ditto, Xichou, SATY0831, LSY; (b5) *Lethe latiaris cenwanga* subspec. nov., HT, Guangxi, Tianlin, SATY0362, CMNH; (b6) ditto, PT, ditto, SATY0832, LSY; (c) *Lethe guansia* SUGIYAMA, 1999, Guangdong, Ruyuan, SATY0540, LSY.



Fig. 24: Valva apex in dorsal view. (a1) *Lethe eitschbergeri* spec. nov., HT, Yunnan, Pingbian, SATY0826, CMNH; (a2) ditto, PT, Yunnan, Malipo, SATY0827, LSY; (a3) ditto, PT, Yunnan, Xichou, SATY0830, LSY; (a4) ditto, PT, Guangxi, Tianlin, SATY0828, LSY; (b) *Lethe eitschbergeri zhujqi* subspec. nov., HT, Yunnan, Dulongjiang, SATY0829, CMNH; (c) *Lethe latiaris* (HEw., 1863), Tibet, Zayu, SATY0484, LSY; (d) *Lethe latiaris lishadii* HUANG, 2002, Yunnan, Gongshan, SATY0833, LSY; (e1) *Lethe latiaris perimele* FRUHST., 1911, Yunnan, Yingjiang, SATY0825, LSY; (e2) ditto, Xichou, SATY0831, LSY; (f1) *Lethe latiaris cenwanga* subspec. nov., HT, Guangxi, Tianlin, SATY0362, CMNH; (f2) ditto, PT, ditto, SATY0832, LSY; (g) *Lethe guansia* SUGIYAMA, 1999, Guangdong, Ruyuan, SATY0540, LSY.



Fig. 25: Distribution map of the *Lethe latiaris* (HEWITSON, 1863)-complex in S.W. China & Indo-China (*L. latiaris hige* FUJIOKA from Nepal is not included; sources of data: Specimens kept in LSY; INAYOSHI's website; LANG, 2017; MONASTYRSKII, 2005; OSADA et al., 1999; SHIZUYA et al., 2005).

Notes on the generic classification of *Lethe* HÜBNER, [1819], *Enodia* HBN., [1819], *Satyrodes* SCUDDER, 1875 and *Zophoessa* DOUBLEDAY, [1849]

(Lepidoptera, Nymphalidae, Satyrinae)

by

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Abstract: In this paper, generic classification of *Lethe* HÜBNER, [1819], *Enodia* HBN., [1819], *Satyrodes* SCUDDER, 1875 and *Zophoessa* DOUBLEDAY, [1849] is studied. There are 2 subgenera recognised in the genus *Lethe* HBN., viz. the subgenus *Zophoessa* DBLD. and the subgenus *Lethe* HBN. Following DE LESSE (1957), Nearctic *Enodia* HBN. and *Satyrodes* SCUDD. are still considered as two species groups of the subgenus *Lethe* HBN., viz. *portlandia*-group and *eurydice*-group respectively. A checklist of the integrated *Lethe* HBN., including its subgenera, groups, subgroups and species, is given. Moreover, morphology of final instar larvae, androconia, o^o genitalia, venations, wing patterns, evolution, zoogeography and phylogeny of the genus *Lethe* HBN. are discussed.

In various literatures and websites, the relationship of Lethe HÜBNER, [1819], Enodia HBN., [1819] and Satyrodes Scudder, 1875 (Satyrini: Lethina) seems uncertain. Excluding Enodia HBN. and Satyrodes SCUDD. from North America, the genus Lethe HBN., including Zophoessa DOUBLEDAY, [1849] as a subgenus, is known from the whole Oriental region, the southeastern frontier of the Palearctic region, and the western corner of the northern Australian region (only one species from the Moluccas). Current researchers who study New World butterflies usually considered Enodia HBN. and Satyrodes SCUDD. as synonyms or subgenus of Lethe HBN. (for example, CARDÉ et al. 1970; SCOTT, 1986; PELHAM, 2012, etc.), but scholars mainly from Old World (for example, D'ABRERA, 1990; BOZANO, 1999; LANG, 2017, 2019b) treated Lethe HBN. as a strict Asian genus which doesn't contain any Nearctic elements. For clarifying this debate, some literatures including those historic works should be reviewed first. Type species of the generic names Lethe HBN., Enodia HBN. and Satyrodes SCUDD. are Papilio europa F., 1775, Oreas andromacha HBN., [1809] (junior synonym of Papilio portlandia F., 1781) and Papilio eurydice L., 1763 respectively. WESTWOOD (1851) arranged europa F. and portlandia F. in Debis DBLD., [1849] (now a junior synonym of Lethe HBN.) and arranged canthus L., 1767 (junior synonym of eurydice L.) in Neonympha HBN., 1818 (Satyrini: Euptychiina). BUTLER (1868) put both europa F. and portlandia F. in Lethe HBN. and put canthus L. (junior synonym of eurydice L.) in Pararge HBN., [1819] (Satyrini: Parargina). In the early years, only few authors alike WESTWOOD (1851) and BUTLER (1868) put members of Enodia HBN. in Lethe HBN., but it seems that nobody realised that Satyrodes SCUDD. is also closely related to Lethe HBN. Until SEITZ's time, the situation had not been changed. When commented on the genus Enodia HBN. in SEITZ's "Gross-Schmett. Erde", WEYMER (1911) stated "Der Rippenverlauf der Falter stimmt mit der indischen Gattung Lethe überein, die Gastalt der Rp ist aber schon dadurch verschieden, dass der Kopf bei Lethe ein Horn, bei Enodia zwei Hörner trägt [The neuration of the butterflies agrees with the Indian genus Lethe, but the shape of the larva differs in that the head in Lethe bears one horn, in Enodia two]". Probably, WEYMER's statement was the origin of that some researchers confirmed that Enodia HBN. and Satyrodes SCUDD. are not members of Lethe HBN. Furthermore, both D'ABRERA (1990) and BOZANO (1999) quoted the statement about the two horns larva of Enodia HBN. and the one horn larva of Lethe HBN. in their own works which have worldwide reputations. Unfortunately, WEYMER's statement was totally based on a mistake, because larvae of Lethe HBN. also have a pair of cephalic horns. Knowledges of the larvae of Lethe HBN. can be learned from a lot of literatures, such as SHIRÔZU & HARA (1960, 1962), HARADA et al. (2005), SHIZUYA & HARADA (2013), etc. Moreover, according to CARDÉ et al. (1970), larvae of Satyrodes Scudd. also bear a pair of cephalic horns alike those of Enodia HBN. Therefore, morphology of larvae cannot provide any difference, nor, conversely, it supports these three generic taxa are closely related. D'ABRERA's series of books since 1980s have been references not only for taxonomists but also for many experts of molecular systematics as well as scholars of other fields, so his viewpoint, that Lethe HBN., Enodia HBN. and Satyrodes Scudd. are three genera, affected a lot of following authors who involved in this topic. Now it is clear that this is an error made by WEYMER (1911) who provided a key but wrong feature of larvae to support Enodia HBN., which is a distinct genus from Lethe HBN. and expanded by D'ABRERA (1990) to the current time. Despite this, also many authors did not follow the error and they had their own considerations on this topic. CHERMOCK (1947) was the first who studied all three genotypes of Lethe HBN., Enodia HBN. and Satyrodes SCUDD., with comparing their of genitalia and venations, and thought that their basic structures are identical. He believed that Enodia HBN. might be used as a subgeneric name of Lethe HBN. and Satyrodes SCUDD, was to be considered as a synonym of Enodia HBN. DE LESSE (1957) in his "Révision du genre Lethe" partly followed CHERMOCK (1947) but he considered both Enodia HBN. and Satyrodes Scupp. as two species groups of Lethe HBN., viz. Portlandia-group and Eurydice-group respectively. Recently, PELHAM (2012) treated both Enodia HBN. and Satyrodes SCUDD. as subgenera of Lethe HBN. Again, WEYMER's (in SEITZ, 1911) influence is so strong and it has been largely amplified by D'ABRERA (1990), so it resulted in that people who know little about the classification of Nearctic butterflies easily trusted these famous books but ignored the truth which had already been found by CHERMOCK (1947), DE LESSE (1957), etc. That is the reason why a lot of authors have treated Enodia HBN. and Satyrodes SCUDD. as distinct genera until now. Now, it is clear that considering *Enodia* HBN. and *Satvrodes* SCUDD. as components of *Lethe* HBN. is highly supported by several original taxonomic studies, but considering Enodia HBN. and Satyrodes SCUDD. as distinct genera is only based upon mistakes. Following DE LESSE (1957), in this study, I continue to treat Enodia HBN. and Satyrodes SCUDD. as two species groups in Lethe HBN., viz. portlandia-group and L. eurydice-group respectively.

The next is Zophoessa DBLD. from Asia. Since its establishment, the concept of Zophoessa DBLD. has not been stable. At first, only its genotype Zophoessa sura DBLD., [1849] was included. In MOORE (1892), Zophoessa DBLD. as an independent genus included members of nowadays sura-subgroup, moelleri-subgroup, jalaurida-subgroup, part of tristigmata-subgroup and even a species of subgenus Lethe HBN., viz. L. gracilis (OBTH.). In SEITZ (1907), it was also a genus, it not only included members of nowadays sura-group but also included some components of current subgenus Lethe HBN., such as members of baladeva-group and L. gracilis

(OBTH.) of gracilis-group. FRUHSTORFER (1911) considered Zophoessa DBLD. as a group in the genus Lethe HBN. but with similar contents of SEITZ (1907). EVANS (1932), followed by TALBOT (1947), treated Zophoessa DBLD. as a junior synonym of Lethe HBN. and proposed the sura-group which equals the scope of nowadays subgenus Zophoessa DBLD. in which all components of the subgenus Lethe HBN. are rightly excluded. DE LESSE (1952) considered Zophoessa DBLD. as a distinct genus and subdivided it into 3 species groups, and from then on, no matter as a genus or a subgenus, the content of Zophoessa DBLD. became steady. Today, the status of Zophoessa DBLD. is still controversy, it is a debate of subgenus (D'ABRERA, 1985, 1990; BOZANO, 1999; LANG, 2017; etc.) against genus (AOKI et al., 1982; etc.). It is nearly undoubted that Zophoessa DBLD. is monophyletic but without it, the genus Lethe HBN. is risked to be a paraphyletic taxon. Therefore, I still considered Zophoessa DBLD. as a subgenus of the genus Lethe HBN.

Material: Specimens in this study are kept in SONG-YUN LANG'S private collection, Shuangliu, Chengdu, CHINA (LSY). Excepting a monotypical species group of the subgenus *Lethe* HBN., viz. *L. dynsate* (HEW., 1863)-group from Sri Lanka, materials of all related subgenera, species groups and subgroups have been examined.

A checklist of the genus Lethe HÜBNER, [1819]

The present checklist mainly follows the classifications of DE LESSE (1957) and LANG (2017) but with some modifications. The orders of groups and subgroups have some adjustments to seek a more natural arrangement. Newly described species are included. Two fossil species with subgenera incertae sedis are also included.

Genus *Lethe* HBN., [1819] I. Subgenus *Zophoessa* DOUBLEDAY, [1849]

Zophoessa DBLD., [1849]. Gen. diurn. Lep. (1): pl. 61: 1. Type species (TS): Zophoessa sura DBLD. Sinchula MOORE, [1892]. Lep. Ind. 1: 275. TS: Debis sidonis Hew. Kerrata MOORE, [1892]. Lep. Ind. 1: 285. TS: Lethe tristigmata ELW. Harima MOORE, [1892]. Lep. Ind. 1: 299. TS: Neope callipteris BTLR. Magula FRUHST., in SEITZ, 1911. Gross-Schmett. Erde 9: 313. TS: Zophoessa jalaurida NICÉV.

I-1. Lethe sura (DBLD., [1849])-group

I-1-1. Lethe sura (DBLD.)-subgroup

L. sura (DBLD.), L. dura (MARSHALL, 1882), L. dataensis (SEMPER, 1887), L. yuemingae LANG, 2014, L. goalpara (MOORE, [1866]), L. labyrinthea LEECH, 1890, L. yoshikoae (KOIWAYA, 2011), L. yantra FRUHST., 1914

I-1-2. Lethe moelleri (ELW., 1887)-subgroup

L. moelleri (ELW.), L. gregoryi WATKINS, 1927, L. helle (LEECH, 1891), L. uemurai (SUGIYAMA, 1994), L. neofasciata LEE, 1985, L. lisuae (HUANG, 2002), L. shirozui (SUGIYAMA, 1997), L. akibai (KOIWAYA & SHIZUYA, 2011), L. kabrua (TYTLER, 1914)

I-1-3. *Lethe procne* (LEECH, 1891)-subgroup *L. procne* (LEECH), *L. paraprocne* LANG & LIU, 2014, *L. changchini* HUANG, 2019

I-1-4. Lethe tristigmata ELWES, 1887-subgroup

L. tristigmata ELW., L. ocellata (POUJADE, 1885), L. baileyi SOUTH, 1913, L. lyncus DE NICÉVILLE, 1897, L. leei H. WANG & ZHAO, 2000, L. nigrifascia LEECH, 1890, L. liyufeii HUANG, 2014, L. luojiani LANG & C. WANG, 2016, L. fasciata SEITZ, 1907, L. baoshana (HUANG et al., 2003), L. armandina (OBERTHÜR, 1881), L. jianqingi LANG, 2016

I-1-5. Lethe jalaurida (NICÉV., 1881)-subgroup

L. atkinsonia (HEWITSON, 1876), L. jalaurida (NICÉV.), L. gelduba FRUHST., 1911, L. elwesi (MOORE, 1892), L. nosei (KOIWAYA, 2000), L. houjiangae LANG & BOZANO, 2015, L. gianchi LANG & DAS, 2020

I-1-6. Lethe sidonis (HEW., 1863)-subgroup

L. sidonis (Hew.), L. maitrya NICÉV., 1881, L. violaceopicta (POUJ., 1884), L. kanjupkula Tyt., 1914, L. burmana Tyt., 1939, L. nicetas (Hew., 1863), L. nicetella NICÉV., 1887, L. cybele LEECH, 1893, L. siderea MARSH., 1881, L. visrava (MOORE, [1866]), L. dakwania Tyt., 1939

I-2. Lethe niitakana (MATSUMURA, 1906)-group

L. niitakana (MATSUM.)

I-3. *Lethe callipteris* (BUTLER, 1877)-group *L. callipteris* (BTLR.)

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II. Subgenus Lethe HBN., [1819]

Argus Scopoli, 1777. Introd. Hist. nat.: 432. TS: Papilio eurydice L. Junior homonym of Argus Bohadsch, 1761 (Mollusca: Gastropoda).

Lethe HBN., [1819]. Verz. bek. Schmett. (4): 56. TS: Papilio europa F.

Enodia HBN., [1819]. Verz. bek. Schmett. (4): 61. TS: Oreas andromacha HBN.

Tanaoptera BILLBERG, 1820. Enum. Ins. Mus. Billb., p. 79. TS: Papilio europa F.

Debis DBLD., [1849]. Gen. diurn. Lep. (1): pl. 61: 3. TS: Debis samio DBLD.

Satyrodes Scudd., 1875. Bull. Buffalo Soc. nat. Sci. 2: 235. TS: Papilio eurydice L. Replacement name of Argus Scop.

Hanipha MOORE, [1880]. Lep. Ceylon 1: 18. TS: Lethe sihala MOORE

Tansima MOORE, 1881. Trans. ent. Soc. Lond. 1881 (3): 305. TS: Lethe satyrina BTLR.

Charma DOHERTY, 1886. J. Asiat. Soc. Bengal 55 (2): 117. TS: Zophoessa baladeva MOORE

Pegada MOORE, [1892]. Lep. Ind. 1: 224. TS: Mycalesis oculatissima POUJ.

Rangbia MOORE, [1892]. Lep. Ind. 1: 232. TS: Debis scanda MOORE

Nemetis MOORE, [1892]. Lep. Ind. 1: 237. TS: Papilio minerva F.

Kirrodesa MOORE, [1892]. Lep. Ind. 1: 237. TS: Debis sicelis Hew.

Placilla MOORE, [1892]. Lep. Ind. 1: 253. TS: Lethe christophi LEECH.

Archondesa MOORE, [1892]. Lep. Ind. 1: 270. TS: Lethe lanaris BTLR.

Choranesa Moore, [1892]. Lep. Ind. 1: 270. TS: Lethe trimacula LEECH.

Dionana MOORE, [1892]. Lep. Ind. 1: 271. TS: Lethe (?) margaritae ELW.

Putlia MOORE, [1892]. Lep. Ind. 1: 287. TS: Zophoessa baladeva MOORE. Unnecessary replacement name of Charma DOH.

Hermias FRUHST. in SEITZ, 1911. Gross-Schmett. Erde 9: 324. TS: Satyrus verma Koll.

II-1. Lethe europa (FABRICIUS, 1775)-group

L. europa (F.), L. arete (STOLL, [1780]), L. rohria F., 1787, L. darena C. & R. FELDER, [1867], L. daretis (Hew., 1863), L. drypetis (Hew., 1863), L. perimede STAUDINGER, [1897], L. violae TSUKADA & NISHIYAMA, 1979

II-2. *Lethe dynsate* (Hew., 1863)-group *L. dynsate* (Hew.)

II-3. Lethe satyrina BTLR., 1871-group

L. satyrina BTLR., L. verma (Kollar, 1844), L. confusa Aurivillius, 1898, L. hyrania (Koll., 1844), L. baucis Leech, 1891, L. kazuichiroi Yoshino, 2008, L. brisanda Nicév., 1886, L. sadona Evans, 1932

II-4. *Lethe marginalis* (MOTSCHULSKY, 1860)-group *L. marginalis* (MOTSCH.)

II-5. Lethe samio (DBLD., [1849])-group L. samio (DBLD.), L. kansa (MOORE, 1857), L. sinorix (Hew., 1863)

II-6. Lethe minerva (F., 1775)-group

L. minerva (F.), L. chandica (MOORE, [1858]), L. mekara (MOORE, [1858]), L. distans BTLR., 1870, L. delila STDGR., [1897], L. dora STDGR., [1897], L. kondoi UÉMURA, 1997, L. manthara (C. & R. FELDER, [1867]), L. vindhya C. & R. FELDER, 1859, L. serbonis (HEW., 1876), L. sicelides GROSE-SMITH, 1893, L. bhairava (MOORE, [1858]), L. gulnihal NICÉV., 1887, L. latiaris (HEW., 1863), L. guansia SUGIYAMA, 1999, L. konkakini MONASTYRSKII & DEVYATKIN, 2000, L. eitschbergeri LANG, 2020, L. melisana MONAST., 2005, L. philesanoides MONAST. & DEVY., 2003, L. mataja FRUHST., 1908, L. berdievi MONAST., 2005, L. camilla LEECH, 1891, L. luyanquani HUANG, 2019, L. privigna LEECH, 1892, L. tengchongensis LANG, 2016, L. christophi LEECH, 1891, L. diana (BTLR., 1866), L. titania LEECH, 1891, L. kouleikouzana YOSHINO, 2008, L. philesana MONAST. & DEVY., 2000, L. satyavati NICÉV., 1881, L. scanda (MOORE, 1857)

II-7. *Lethe laodamia* LEECH, 1891-group *L. laodamia* LEECH, *L. philemon* FRUHST., 1902

II-8. *Lethe syrcis* (Hew., 1863)-group *L. syrcis* (Hew.), *L. inomatai* KOIWAYA, 1989

II-9. Lethe baladeva (MOORE, [1866])-group L. baladeva (MOORE), L. ramadeva (NICÉV., 1887), L. luteofasciata (POUJ., 1884), L. albolineata (POUJ., 1884), L. andersoni (ATKINSON, 1871), L. argentata (LEECH, 1891), L. yunnana D'ABRERA, 1990, L. hayashii KOIWAYA, 1993, L. margaritae (ELW., 1882)

II-10. *Lethe gracilis* (OBERTHÜR, 1886)-group *L. gracilis* (OBTH.), *L. cyrene* LEECH, 1890, *L. hecate* LEECH, 1891

II-11. *Lethe sicelis* (Hew., 1862)-group *L. sicelis* (Hew.)

II-12. *Lethe oculatissima* (POUJADE, 1885)-group *L. oculatissima* (POUJ.)

II-13. *Lethe portlandia* (F., 1781)-group *L. portlandia* (F.), *L. anthedon* (CLARK, 1936), *L. creola* (SKINNER, 1897)

II-14. *Lethe eurydice* (LINNAEUS, 1763)-group *L. eurydice* (L.), *L. appalachia* CHERMOCK, 1947

II-15. Lethe lanaris BTLR., 1877-group L. lanaris BTLR., L. naga DOH., 1889, L. huongii Monast., 2004

II-16. Lethe trimacula LEECH, 1890-group L. trimacula LEECH, L. proxima LEECH, 1892, L. langsongyuni S. HUANG et al., 2019, L. umedai KOIWAYA, 1998, L. liae HUANG, 2002, L. butleri LEECH, 1889

II-17. Lethe manzorum (Pouj., 1884)-group L. manzorum (Pouj.), L. sisii Lang & Monast., 2016, L. gianchozanoi Lang & Monast., 2016, L. langyii Lang, 2019, L. monilifera Obth., 1923

II-18. *Lethe gemina* LEECH, 1891-group *L. gemina* LEECH

III. Fossil species

L. (?) corbieri A. NEL, J. NEL & BALME, 1993 L. montana J. MILLER, L. MILLER & IVIE, 2012

Final instar larvae

I do not have any experience on study of immature stages of butterflies, but luckily fine figures and photographs of larvae of the genus Lethe HBN. can be found from abundant literatures by a lot of scholars, such as SHIRÔZU & HARA (1960, 1962), CARDÉ et al. (1970), SHIZUYA & HARADA (2013), HARADA et al. (2005), LU & CHEN (2014), etc. In the following text, only final (5th) instar larva stage is discussed (next simply as larva). Larvae of both the subgenus Zophoessa DBLD. and the subgenus Lethe HBN. (including its Nearctic species) have a pair of developed cephalic horns, and no obviously structural differences can be found between them. Comparatively, as a very closely related genus of Lethe HBN., larvae of the genus Neope MOORE, [1866] are quite different. Larvae of Neope MOORE have rounded heads in front view which bear a pair of only very slightly raised cephalic horns (or totally absent in some species), whereas in the genus Lethe HBN., including its 2 subgenera, larvae have trapezoid or square heads in front view which bear a pair of well developed cephalic horns. In SHIRÔZU & HARA (1960: plate 15) L. callipteris (BTLR.) (subgenus Zophoessa DBLD.) has a somewhat trapezoid head bearing a pair of shorter and blunt horns. In Lu & CHEN (2014: 461), cephalic horns of L. dura (MARSH.) (subgenus Zophoessa DBLD.) are sharply pointed. According to CARDÉ et al. (1970: 87), both L. eurydice (L.) and L. appalachia CHERM. (subgenus Lethe HBN.) from N. America have trapezoid heads bearing sharply pointed horns. Certainly, extreme exception also can be found. In HARADA et al. (2005), larva of L. siderea MARSH. (Subgenus Zophoessa DBLD.: suragroup: sidonis-subgroup) does not have a pair of visible cephalic horns, but its head is still trapezoid in front alike other species of Lethe HBN. Moreover, ZHU et al. (2018) illustrated a larva of L. violaceopicta (POUJ.) (sidonis-subgroup) which has a pair of well developed horns on its head. Therefore, the missing of cephalic horns from the head of L. siderea MARSH. is because of a secondary degeneration. According to photographs of SHIRÔZU & HARA (1960: plate 15), the head of Ninguta schrenkii (MÉNÉTRIÈS, 1859), the monotypic species of Ninguta MOORE, 1892 form E. Asia, is very similar to L. marginalis (MOTSCH.) (subgenus Lethe HBN.), and both of them have a nearly square head bearing a pair of elongated and sharply pointed horns. The similarity of larvae of Ninguta MOORE and Lethe HBN. is probably symplesiomorphous. Because larvae like Lethe HBN. also can be found from other related genera such as Ninguta MOORE (mentioned above) and Orinoma hainanensis (KOIWAYA, 1993) (HARADA et al., 2012), larva head morphology cannot be considered as a synapomorphy or shared derived character of Lethe HBN.

Androconia

The basic type of androconia from forewing upperside of the tribe Satyrini, the main clade of the subfamily Satyrinae, has four parts from top to base as following: terminal ears, distal stalk, lamina and basal stalk (LANG, 2019a modified from WAKEHAM-DAWSON & KUDRNA, 2000). Here, I call this basic type as "Satyrini-type". In this reasearch, "Satyrini-type" of androconia (Fig. 1: b-i, 11-118) has been found from 8/13 subtribes in Satyrini including Lethina, Parargina, Coenonymphina, Maniolina, Satyrina, Ypthimina, Erebiina and Euptychiina. Though their shapes can vary in a large degree, the basic model is not changed. "Satyrinitype" scale might be derived from its ancient type more earlier before the arising of Satyrinae, because androconia with similar appearance have also been found from forewing upperside of the genus Argynnis F., 1807 (Fig. 1: a) of the nymphalid subfamily Heliconiinae. Probably, the origin of "Satyrini-type" was together with the appearing of the clade which includes most modern subfamilies of Nymphalidae only excepting Libytheinae and Danainae. In subtribe Lethina which includes Lethe HBN. and its relative genera, the appearance of this kind of androconia is normal in the genus Neope MOORE (Fig. 1: i) and in the subgenus Lethe HBN. (Fig. 1: 11-118). Nevertheless members of the subgenus Zophoessa DBLD. have quite different shaped androconium scales (Fig. 1: z1-z12). When studying androconia of Polyommatinae (Lycaenidae), ELIOT (1973) once said "using the term [androconia] in a wide sense to indicate any type of scale not found in the female". So, it is sound that different types of androconium scales of butterflies are analogous but not homologous organs. The or butterflies of primative groups of Zophoessa DBLD. (callipteris-group and niitakana-group) have very developed transverse brands on forewing upperside, but their androconium scales from the brands with nearly no specialized structures look alike those ordinary scales. Here I treat them as the "Zopho-archetype" (Fig. 1: z1, z2). In sura-group, there are 3 tpyes of androconia derived from "Zopho-archetype" can be recoginsed: "Zopho-Type I" (Fig. 1: z12) with a weakly bifurcated top and a pair of round lobes (this type is very close to "Zopho-archetype", and now is only found from L. leei WANG & ZHAO of tristigmata-subgroup); "Zopho-Type II" (Fig. 1: z8-z11) with a deaply bifurcated apex and a pair of acute tips (occasionally trifurcated) (this type is found from most species of tristigmata-subgroup and few species of jalaurida-subgroup (my Indian colleague Das examined androconia of L. atkinsonia (HEW.) and L. elwesi (MOORE) from Sikkim)); "Zopho-Type III" (Fig. 1: z3-z7) with a row of 3 to 10 regularly arranged spines on the top (this type is found from *sura*-subgroup, *moelleri*-subgroup and procne-subgroup). Most possibly as mentioned above, and roconium scales of "Satyrini-type" and "Zopho-archetype" and its descendent types are only analogous organs which had been evolved separately. The "Satyrini-type" androconia had lost in the ancestor stem of Zophoessa DBLD. and latter some ordinary scales evolved with a similar function of scent scales. With the flurish of this clade, kinds of new androconia derived from the "Zopho-archetype" came out in Zophoessa DBLD. Therefore, knowledge of androconia of Zophoessa DBLD. suggests that this subgenus is a comparatively young clade in the genus Lethe HBN. In the subgenus Lethe HBN., the "Satyrini-type" scent scales (Fig. 1: 11-118) also have some modifications at different levels in

In the subgenus *Lethe* HBN., the "Satyrini-type" scent scales (Fig. 1: 11-118) also have some modifications at different levels in some species groups. In *europa*-group, an obvious distal stalk cannot be found from androconia of *L. europa* (F.) and *L. rohria* F. (Fig. 1: 11, 12). It seems that androconia of *satyrina*-group have both terminal ears and distal stalk absent. I found a kind of scale from the forewing upperside of *L. satyrina* BTLR. (Fig. 1: 13) which is similar to androconia of *L. confusa* AURIV. illustrated by AOKI et al. (1982: 235: fig. c), but I did not find such scale from Chinese specimen of *L. confusa* AURIV. Moreover I checked other species of *satyrina*-group, only excepting *L. sadona* EVANS, but no obviously characterised androconium scale can be found from them. However, I'm still not sure this kind of scale (Fig. 1: 13) from *satyrina*-group is a true scent scale. The lamina of *marginalis*-group (Fig. 1: 117, 118) are very similar, their laminae are small with developed and brush-like terminal ears on top and with distal stalk absent. The lamina of *gemina*-group (Fig. 1: 116) is deeply concaved at its bottom. However, in subgenus *Lethe* HBN., androconium scales of most species groups have a little structural modification comparing with the basic model of "Satyrini-

type". It is worth mentioning that androconia of Nearctic *portlandia*-group (Fig. 1:114) is similar to the monotypical *oculatissima*group (Fig. 1:113) from China, and both of them have a very short distal stalk and a short vase-like lamina. In this research the androconia of the monotypical *dynsate*-group from Sri Lanka is not checked, and androconium scale has not been found from forewings of *eurydice*-group and *lanaris*-group in the subgenus *Lethe* HBN.

Male genitalia

DE LESSE (1957) discussed generic differences of σ genitalia of subgenus *Zophoessa* DBLD. (as a distinct genus in his work) and subgenus *Lethe* HBN. Structure of σ genitalia of Nearctic clade, viz. *portlandia*-group and *eurydice*-group, has no significant difference comparing with those of most species groups of the subgenus *Lethe* HBN. from Asia, and, therefore, it is reasonable to treat them as members of the subgenus *Lethe* HBN. Some features of σ genitalia should be emphasized in the following text. The first is the pedunculi and the appendices angulares (app.ang.) (KLOTS, 1970) which are two paired processes arising from laterocaudal tegumen. In DE LESSE (1957), these two structures were simply treated as tegumen. The second are the apical slices of the aedoeagus which were not mentioned in DE LESSE (1957).

♂ genitalia of the subgenus Zophoessa DBLD. (Fig. 2: a-c): Tegumen: the pedunculi very short or with caudal edge concaved; the app.ang. rather narrow, briefly prolonged along the vinculum, then forming hooked lobes, protruding backwards. Uncus: usually more or less bulged and bumpy towards the base or the middle. Gnathos: usually long. Valva: broadly triangular (in triangle often almost isosceles), with the tip generally swollen and circumvented. Saccus: short. Aedoeagus: short, almost always bent up sharply in the middle.

♂ genitalia of the subgenus *Lethe* HBN. (Figs. 2, 3: d-x): Tegumen: the pedunculi broad and elongated; the app.ang. broadly extending along the vinculum and ending briefly in short lobes. Uncus: robust with regular dorsal contour or forming a ridge sometimes very developed. Gnathos: often slender, short, or absent. Valva: triangle, elongated towards the end, not isosceles in general. Saccus: elongated. Aedoeagus: always straight and usually elongated; the dorsal and ventral walls of the aedoeagus are invaginated into the vesica for a long distance, forming a pair of upper and lower apical slices which are absent in *manzorum*-group, *gemina*-group, and subgenera *Zophoessa* DBLD.

Venations

According to TALBOT (1949), forewing upper angle of the cell is evenly rounded and forewing vein 12 is terminated at a point above the end of the cell in the subgenus *Zophoessa* DBLD., whereas the upper angle of the cell is angled and vein 12 is terminated at a point well beyond end of the cell in the subgenus *Lethe* HBN. (Table 1). The venations of Nearctic *portlandia*-group and *eurydice*-group fall into the category of the subgenus *Lethe* HBN.., and, therefore, it is again to support that they are species groups of the subgenus *Lethe* HBN. The venation of *Ninguta* MOORE is very close to the subgenus *Lethe* HBN., however, its hindwing vein 1a is nearly as long as vein 1b, whereas hindwing vein 1a is much shorter and about half to two thirds as long as the vein 1b in *Lethe* HBN. and *Neope* MOORE. Moreover, evenly rounded forewing upper angle of the cell can be treated as a synapomorphy of the subgenus *Zophoessa* DBLD.

A swollen base of forewing vein 12, cubitus and vein 2a is an apomorphy of Satyrinae, but satyrid butterflies in which the veins are not swollen are not uncommon. When discussed fossils of *Lethe* HBN., DE JONG (2017) mentioned swelling of veins and according to him, "In extant *Lethe* there are no basally swollen veins in the forewing; at most, Sc [vein 12 in the present paper] is thicker in its proximal part than the radius, or fused with the proximal part of the radius to a thicker vein. It is uncertain if such a subtle difference is clearly visible in a fossil". In fact, in a comparatively large genus, the situation is not simple. Indeed, the genotype of *Lethe* HBN., viz. *L. europa* (F.), has no obviously swollen veins of the forewing. However, usually, species has an obviously basally swollen vein 12, such as *L. laodamia* LEECH, *L. syrcis* (HEW.), etc. It seems that the swelling degree of vein 12 varies in the genus from nearly invisible to strongly swollen. Moreover, *L. yantra* FRUHST. has heavily basally swollen vein 12 and cubitus as well as weakly swollen vein 2a. Therefore, the presence or absence of swollen veins cannot act as a diagnostic character to determine whether a fossil is or is not a member of the genus *Lethe* HBN.

Taxa	Genus Neope	Genus Ninguta	Genus Lethe	
Characters			Lethe	Zophoessa
forewing upper angle of the cell	smooth and oblique	angled	angled	evenly rounded
forewing vein 12	terminated at a point beyond the end of the cell	terminated at a point well beyond the end of the cell	terminated at a point well beyond the end of the cell	terminated at a point above the end of the cell
hindwing vein 8	nearly as long as the vein 7	obviously shorter than the vein 7	about half as long as the vein 7	about half as long as the vein 7
hindwing vein 1a	about half to two thirds as long as the vein 1b	nearly as long as the vein 1b	about half to two thirds as long as the yein 1b	about half as long as the vein 1b

Table 1. Characters of venation of Neope MOORE, [1866], Ninguta MOORE, 1892 and Lethe HBN., [1819].

Wing patterns

In most species of the genus *Lethe* HBN., forewing underside with a couple of dark bands in the cell, but in *sidonis*-subgroup (subgenus *Zophoessa* DBLD.: *sura*-group) and *gemina*-group (subgenus *Lethe* HBN.) dark band in the cell of forewing underside is absent, in *marginalis*-group, *oculatissima*-group, *sicelis*-group, *lanaris*-group, *trimacula*-group, *portlandia*-group and *eurydice*-group of subgenus *Lethe* HBN. only one band present in the cell of forewing underside. Comparatively, number of hindwing underside bands in the cell can provide more useful information in subgeneric classification. According to TALBOT (1949), hindwing underside has more than one band in the cell in the subgenus *Zophoessa* DBLD., whereas it has not more than one (0-1) band in the cell in the subgenus *Lethe* HBN. Both Nearctic *portlandia*-group and *eurydice*-group have only one band in the cell on the hindwing underside as other subgenus *Lethe* HBN. from Asia.

Evolution

Fossil records of Satyrinae are very rare, but it happened that 2 fossil species of Lethe HBN. have been discovered, they are L. (?) corbieri NEL, NEL & BALME from S.E. France and L. montana MILLER, MILLER & IVIE from Montana, USA (Fig. 4). According to DE JONG (2017), both fossils were excavated from the early Oligocene deposits (Rupelian Age from 33.9 to 28.1 Mya). Of course, it might be inaccurate that putting the fossil specimens into the extant genus Lethe HBN. based on phenetic similarities, but, without adverse evidences, they are still important clues of the evolution of Lethe HBN. MILLER (1968) stated that "... Enodia portlandia and creola, Satyrodes eurydice, ..., appear to be pre-Pleistocene arrivals; these butterflies probably arrived in North America in the Miocene or Pliocene, perhaps even earlier". MILLER's speculation agrees well with the fossil records of Lethe HBN. which were excavated decades latter. Basing upon the above mentioned information, an early evolution figure of Lethe HBN. can be roughly outlined. Because of extant species richness and diversity in Asia, Lethe HBN. was most likely originated in eastern Palaearctic (Asia). During Oligocene (ca. 34 to 23 Mya), ancestors of Lethe HBN. had been reached the westernmost of Eurasia (western Palaearctic) and N. America (Nearctic). Nowadays, the genus had been totally disappeared from western Palaearctic but it still has representatives, viz. portlandia-group and eurydice-group, in eastern Nearctic. It is said that the extant distribution pattern of the genus Lethe HBN. is a typical "eastern North America-Asia disjunction" (Fig. 4). Now, the question is how its ancestors went to Nearctic from Palaearctic? According to SANMARTÍN et al. (2001), "faunal (and floral) exchange between Asia and eastern North America could have taken place via two different routes: either across Beringian Bridge or across the Thulean Bridge (which is supposed to have connected southern Europe to Greenland through the British Isles). An important difference between these two hypotheses is in the predicted age of the disjunction. Trans-Beringian dispersal in warm-temperate groups presumably peaked during the warm period in the Eocene, which ended in the terminal Eocene event (about 35 Mya), whereas trans-Atlantic dispersal was unlikely after the breakup of the Thulean Bridge (about 50 Mya)". Therefore, considering the ages of fossils, as subtropical distributed organisms, ancestors of Lethe HBN. might disperse to N. America through Beringian Bridge about 35 Mya, i.e. before the end of Eocene (Of course, this conclusion is about 10 million years earlier than the results of some recent molecular systematics). Furthermore, more likely the remnants of Lethe HBN. in western Palaeoarctic were finnally wiped out during the periods of Pleistocene glaciations.

Zoogeography

The subgenus *Lethe* HBN. has more than 80 species from eastern Old World besides its Nearctic components (2 groups 5 species). Its core distributional area with the highest biodiversity is the Sino-Himalayan region including S.W. China, N. India and N. Indo-China (especially N. Myanmar). Most species groups with their elements are known from Sino-Himalayan region, excepting the *europa*-group (most its species from Malay Archipelago) and other two monotypical groups, viz. *sicelis*-group and *dynsate*-group from Japan and Sri Lanka respectively.

The subgenus *Zophoessa* DBLD. seems to be a young clade in the genus *Lethe* HBN. and its absence from N. America probably indicates that when *Lethe* HBN. migrated to New World about 35 Mya, *Zophoessa* DBLD. was not emerged on the earth. There are 3 species groups of the subgenus *Zophoessa* DBLD., and among them 2 monotypical groups are isolatedly distributed on Nihon retto-Sakhalin Is. and Taiwan Is. respectively. Most species of *Zophoessa* DBLD. belong to *sura*-group which distributes in Sino-Himalayan region but with a single species known from N. Luzon Is., viz. *Lethe dataensis* (SEMPER). Comparing with their Sino-Himalayan congeners in the subgenus *Zophoessa* DBLD., monotypical *callipteris*-group and *niitakana*-group seem to be more primative. The *callipteris*-group with only *Lethe callipteris* (BTLR.) is known from Japanese archipelago and south Sakhalin where no other species of *Zophoessa* DBLD. is known. The *niitakana*-group, with only *Lethe niitakana* (MATSUM.), is known from Taiwan Is. where only two other *Zophoessa* DBLD. species belonging to *sura*-group are recorded. Though there are more than 40 species of the subgenus *Zophoessa* DBLD. from Sino-Himalayan region, but primative forms alike *callipteris*-group and *niitakana*-group are absent here. Most possibly, during its early flourishing, primative *Zophoessa* DBLD. colonised the whole E. Asia including surrounding islands such as Nihon retto, Sakhalin and Taiwan. After the rising of the more advanced *sura*-group, the primative groups had been replaced and only left their remnants on some geographically remote and isolated islands.

Phylogeny

Basing upon molecular data (4435 bp of DNA sequences from mitochondrial and nuclear genes), PEÑA et al. (2011) recognised the clade ((*Rhaphicera, Neope*), (*Ninguta, (Lethe, (Enodia, Satyrodes*)))) in Satyrini. In their work, the representative of *Lethe* HBN. was only one species, viz. *L. minerva* (F.) of the subgenus *Lethe* HBN. A clade including Nearctic *portlandia*-group and *eurydice*-group (*Enodia* HBN. and *Satyrodes* SCUDD.) and a member of the subgenus *Lethe* HBN. from Asia once again supports that Nearctic taxa are groups of the subgenus *Lethe* HBN. The result of their work supports that *Ninguta* MOORE is the sibling clade of the genus *Lethe* HBN. In a very recent research, LIU et al. (2020) built a phylogenetic tree inferred from mitogenomes for 264 butterfly species in which a clade related to Lethina was exactly present, viz. (*(Neope pulaha, Ninguta schrenckii* [sic]), (*Lethe dura, L. albolineata*)). Considering their generic and subgeneric attributes, the clade can be understood as ((genus *Neope*, genus *Ninguta*), (subgenus *Zophoessa*, subgenus *Lethe*). It is a clue that the subgenus *Zophoessa* DBLD. and the subgenus *Lethe* HBN. are indeed sister groups. However, it also reflects that *Ninguta* MOORE is not sister group of *Lethe* HBN. but is sister group of the genus *Neope*.

To build a clear and perfect phylogenetic tree of the genus *Lethe* HBN. basing upon pure morphological characters is almost impossible. So here I can only draw a rough and tentative phylogenetic tree for the genus *Lethe* HBN., in which synapomorphies only can be limitedly used to support some clades (Fig. 5). The clade containing the genus *Lethe* HBN. as a whole (including subgenus *Lethe* HBN. and subgenus *Zophoessa* DBLD.) suprisingly has no synapomorphy to support itself right now. Probably, their similar features including those of the larvae (final instar larvae with trapezoid or square head in front view which bear a pair of well developed cephalic horns) are symplesiomorphies but not synapomorphies. The clade of the subgenus *Zophoessa* DBLD. can be well supported by several shared derived characters ("*Zopho*-archetype" and its descendent androconia; pedunculi very short or with caudal edge concaved; app.ang. rather narrow, briefly prolonged along the vinculum, then forming hooked lobes, protruding backwards; forewing upper angle of the cell evenly rounded). In the subgenus *Zophoessa* DBLD., 2 clades in *sura*-group can be well supported by their derived and unique shaped androconia from "*Zopho*-archetype", they are (*tristigmata*-subgroup, *jalaurida*-subgroup) and (*sura*-subgroup, *moelleri*-subgroup, *procne*-subgroup). For the current subgenus *Lethe* HBN., it seems that there is no

synapomorphy which can be used to support it, but excepting its *manzorum*-group and *gemina*-group to the remaining components of the subgenus *Lethe* HBN. including the Nearctic clade share a derived charater (the dorsal and ventral walls of the aedoeagus invaginated into the vesica for a long distince, forming a pair of upper and lower apical slices). Probably, establishing a new subgenus for *manzorum*-group and *gemina*-group would be a solution, but to support it, further molecular phylogenetic work is required. All we mordern taxonomists or systematic biologists are nearly supporters of W. HENNIG and his theory. However, in our practices, we do much better when we work on higher categories, and, then, we try to seek a natural classification. But when we work on lower categories, including generic and specific levels, it is possible that we are making more and more paraphyletic taxa. For example, after description of an additional genus from a known genus, the remnant genus is usually risked to be a paraphyletic taxon. Furthermore, after raising some island subspecies to a specific status, the left species with more large population and wide range from mainland will be a paraphyletic species, or is it the reality that: HENNIG' theory is only idealistic rather than pragmatic in the taxonomy at a specific level?

Postscript: In the last year, the Butterfly Society of Japan invited me to make a special invited lecture in the annual meeting 2019. My lecture was entitled as "An introduction of the genus *Lethe* HÜBNER from China". However, when I was preparing a powerpoint of the lecture, I suddenly found that I knew little about the genus as a whole in fact. During my visit in Tokyo, Mr. MASUI and Mr. KURIYAMA from the Society kindly gifted me series of specimens of Japanese *Lethe* HBN. Although only 5 species of the genus have been known from Japan, among them, 2 species belong to their own monotypical species groups respectively. After going back home, I bought 4 Nearctic species from an American sellers on eBay website. Then, in this way, plus comparatively rich Chinese *Lethe* HBN. collection in my own hand, I can finally finish the present paper. Of course, it is only a preliminary discussion. Actually, phylogeny of *Lethe* HBN. is still poorly known, and, on the other hand, new species can still be discovered. When I visited the wonderful collection. I think my Japanese friends are studying it right now. Moreover, in this year, I have published two new species of *Lethe* HBN. in other works. Until now, 143 extant *Lethe* HBN. species have been known worldwide, and among them 109 are recorded from China. As a result, now, in China, there are more and more amateurs who are favorite in collecting *Lethe*-butterflies. I think that it is a fascination for species richness and biodiversity.

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Fig. 1: Androconia. (a) Argynnis xipe niraea OBTH., 1912, China, Sichuan, Kangding; (b) Geitoneura klugi (GUERIN-MENEVILLE, [1831]), Australia, Mt. Mackinzeii; (c) Palaeonympha opalina BTLR., 1871, China, Shaanxi, Zhouzhi; (d) Ypthima dohertyi cenwanga LANG, 2018, China, Guangxi, Tianlin; (e) Loxerebia albipuncta (LEECH, 1890), China, Hubei, Enshi; (f) Aulocera iole songi LANG, 2019, China, Qinghai, Gyegu; (g) Kirinia epimenides (MEN., 1859), China, Shaanxi, Ningshan; (h) Chonala house LANG et al., 2017, China, Chongqing, Nanchuan; (i) Neope fusca LEECH, 1891, China, Shiganxi, (z1-12) Subgenus Zophoessa DBLD; (z1) Lethe nitiakana (MATSUM, 1906), China, Taiwan, Huualian; (z2) L callipteris (BTLR., 1877), Japan, Giitu, Takayama; (z3) L sura (DBLD., [1849]), China, Yunnan, Pingbian; (z4) L yoshikoae (KOWAYA, 2011), China, Zhejiang, Lin'an; (z5) L neofasciata LEE, 1985, China, Yunnan, Dali; (z6) L uemurai (SUGIYAMA, 1994), China, Shaanxi, Fengxian; (z7) L paraprocee LANG & LU, 2014, China, Sichuan, Ebian; (z8) L luojiani LANG & WANG, 2016, China, Shaanxi, Ningshan; (e2) L fasciata SETZ, 1907, China, Shaanxi, Sichuan, Ebian; (z10) L nigrifascia LEECH, 1890, China, Guzhang; (z11) L ocellata (POUJ, 1885), China, Sichuan, Omei; (z12) L leei WANG & ZHAO, 2000, China, Shaanxi, Fengxian; (11-8) Subgenus Lethe HBNS; (1) L europa beroe (CRAMER, [1775]), China, Guangxi, Gugang; (12) L rohria F, 1787, China, Yunnan, Baoshan; (13) L saryrina BTLR., 1871, China, Hunan, Yongshun; (H) L marginalis (MOTSCH, 1860), Japan, Yamnanshi, Anayama; (15) L sinorix (HEW, 1863), China, Tibet, Medog; (16) L mekrar crijnama FRUHST, 1911, China, Hunan, Yongshun; (14) L marginalis (MATSCH, 1860), Japan, Yamnanshi, Casuki; (110) L hayashii KOWAYA, 1994, China, Ganay, Kangxian; (111) L cyrene LEECH, 1890, China, Ganay, Kangxian; (112) L sieelis (HEW, 1863), Japan, Yamnanshi, Gusayi, Jinxiu; (110) L, hayashii KOWAYA, 1994, China, Ganay, Kangxian; (113) L oyalashaya, (114) L portlandia (F, 1781), USA, North Carolina, Craven; (115) L proxima LEECH



Fig. 2: d' genitalia. m.l. - d' genitalia in lateral view with left valva and aedoeagus removed; ped - pedunculi; a.a. - appendices angulares (app.ang.); vin - vinculum; t.d. - tegumen, uncus and gnathos in dorsal view; a.l. - aedoeagus in lateral view; a.d. - aedoeagus in dorsal view; v.d. - left valva in dorsal view; v.a. - left valva apex in dorsal view; ju. - juxta. (a) *Lethe sura* (DBLD., [1849]), China, Yunnan, Pingbian; (b) *L. niitakana* (MATSUM., 1906), China, Taiwan, Hualian; (c) *L. callipteris* (BTLR., 1877), Japan, Gifu, Takayama; (d) *L. rohria* F., 1787, China, Yunnan, Simao; (e) *L. europa beroe* (CR., [1775]), m.l., China, Guangxi, Guigang, a.l. & a.d., China, Jiangxi, Longnan; (f) *L. satyrina* BTLR., 1871, China, Hunan, Yongshun; (g) *L. marginalis obscurofasciata* HUANG, 2002, China, Yunnan, Weixi; (h) *L. sinorix* (HEW., 1863), China, Tibet, Medog; (i) *L. minerva tritogeneia* FRUHST., 1911, China, Yunnan, Mengla; (j) *L. diana* (BTLR., 1866), China, Anhui, Yuexi; (k) *L. laodamia* LEECH, 1891, China, Guizhou, Jiangkou; (l) *L. syrcis* (HEW., 1863), China, Guangxi, Jinxiu.



Fig. 3: & genitalia. (m) Lethe sicelis (HEW., 1862), Japan, Yamanashi, Otsuki; (n) L. baladeva (MOORE, [1866]), China, Tibet, Nyalam; (o) L. gracilis (OBTH., 1886), China, Yunnan, Gongshan; (p) L. oculatissima (POUJ., 1885), China, Sichuan, Yanbiar; (q) L. portlandia (F., 1781), USA, North Carolina, Craven; (r) L. anthedon (CLARK, 1936), USA, New Jersey, Sussex; (s) L. eurydice (L., 1763), USA, New Jersey, Sussex; (t) L. appalachia CHERM., 1947, USA, Alabama, Talladega NF.; (u) L. lanaris BTLR., 1877, China, Shaanxi, Ningshan; (v) L. trimacula LEECH, 1890, China, Sichuan, Hongya; (w) L. gemina gafuri (TYTLER, 1914), China, Tibet, Medog; (x) L. manzorum (POUJ., 1884), China, Sichuan, Ebian.



Fig. 4: Distribution map of the genus Lethe HBN., [1819] worldwide. Blue shadow - the extant range of the genus Lethe HBN.; red cross - fossil record of Lethe HBN.



Fig. 5: A phylogenetic tree of the genus *Lethe* HBN., [1819]. ①-③ Shared derived character(s) supporting its corresponding clade. ① "*Zopho*-archetype" and its descendent types of androconia; pedunculi very short or with caudal edge concaved; app.ang. rather narrow, briefly prolonged along the vinculum, then forming hooked lobes, protruding backwards; forewing upper angle of the cell evenly rounded. ② "*Zopho*-Type I-III" derived from "*Zopho*-archetype". ③ The dorsal and ventral walls of the aedoeagus invaginated into the vesica for a long distince, forming a pair of upper and lower apical slices.

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