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云南保山盆地新近纪云杉属针叶化石及其古海拔指示意义*

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提要　松科(Pinaceae)云杉属(*Picea* A. Dietrich)花粉化石记录丰富，大化石则以木材和球果居多，而针叶化石报道较少且缺少微形态研究。云南保山盆地新近纪羊邑组产大量三维立体保存的云杉属针叶化石。这些针叶化石呈扁平条形，叶尖急尖，叶基截形，无叶柄；上表面中脉隆起，中脉两侧各有一个气孔带，每个气孔带有5–6条气孔线，气孔线多连续，少数不连续，气孔呈椭圆形至长椭圆形，非气孔带表皮细胞矩形至长矩形，细胞壁波浪状弯曲；下表面中脉亦隆起，无气孔，表皮细胞多为矩形至长矩形，细胞壁波浪状弯曲。通过与现生云杉属针叶的宏观形态和微形态对比发现，该化石与油麦吊云杉(*Picea brachytyla* var. *complanata* (Mast.) W. C. Cheng ex Rehder)在形态上最为相似。但由于缺少其他植物器官(如球果)，难以判断化石是否真正代表了这个现生种，因此，将其暂定为似油麦吊云杉。基于云杉属在青藏高原东南缘的海拔分布范围(2000–4000 m)，以及考虑到新近纪比现在更为温暖的气候环境，推测保山盆地在新近纪时期具有比现在(1650 m)更高的海拔。该推断进一步丰富了青藏高原东南缘的海拔演变历史。

关键词　保山盆地　新近纪　云杉属　叶表皮　古海拔　气孔

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Neogene *Picea* leaves from the Baoshan Basin of Yunnan and their implication for paleoaltimetry

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Abstract　*Picea* A. Dietrich. (Pinaceae) has a rich fossil pollen record. Macrofossils of the genus known to date are mainly represented by wood and seed cones, while leaves are scarce. Moreover, reported fossil leaves lack microscopic

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examinations, limiting their taxonomic resolution. In this study, we report a large number of three-dimensional preserved leaves and leaf fragments from the Neogene (latest Miocene to early Pliocene) Yangyi Formation of the Baoshan Basin, western Yunnan Province. These fossil leaves are compressed and flattened. The leaf apex is acuminate and its base is truncated with no petiole. The midvein is obviously raised on both the adaxial and abaxial surfaces. On the adaxial surface, a stomatal band is present on both sides of the midvein, each comprising five or six, mostly continuous stomatal files. The epidermal cells are rectangular to elongate with undulate anticlinal walls. On the abaxial surface, stomata are absent, and the epidermal cells are rectangular to elongate with undulate anticlinal walls. Based on comparisons of gross leaf morphology and micromorphology with extant species of *Picea*, we found that the fossil leaves are most similar to *Picea brachytyla* var. *complanata* (Mast.) W. C. Cheng ex Rehder. Due to the absence of other associated plant organs, it is uncertain if these leaves truly represent this living species. In consequence, we tentatively assign these fossil leaves to *Picea brachytyla* var. *complanata* (Mast.) W. C. Cheng ex Rehder. Based on modern altitudinal range (2000–4000 m) of *Picea* in Yunnan along the southeastern margin of the Tibetan Plateau, the Baoshan Basin might have reached a considerably high elevation, at least higher than the modern level (1650 m), during the latest Miocene and the early Pliocene. Given the warmer climate of that period, *Picea* may have occupied even higher elevations than their modern counterparts. This finding enriches our knowledge on the elevation history of the southeastern margin of the Tibetan Plateau.

Key words　Baoshan Basin, Neogene, *Picea*, leaf epidermis, paleoelevation, stomata

1　引　言

云杉属(*Picea* A. Dietrich)是松科(Pincaceae)的第三大属，仅次于松属(*Pinus* L.)和冷杉属(*Abies* Mill.) (Wright, 1955; Schmidt, 1989; Yang *et al*., 2022)。云杉属约有34种，遍布整个北半球。亚洲有23种，是云杉属物种多样性最高的地区(岑庆雅等, 1996; Wright, 1955; Farjon, 1990, 2001; Fu *et al*., 1999)。我国有云杉属17种，主要分布于东北、华北、西北、西南地区及台湾的高山地带(Farjon, 2001; Ran *et al*., 2006)。青藏高原东南缘有云杉属6种，是该属的重要分布中心(应俊生，1989; 蒋雪彬等, 2000; 刘增力等, 2002; 袁睿佳等, 2007; 李果等, 2009; 李贺等, 2012; Fu *et al*., 1999; Farjon, 2001)。

云杉属有着丰富的化石记录，其中以花粉最为常见，广泛出现于北半球整个新生代地层(Xu *et al*., 2008; Grímsson *et al*., 2011; Xiao *et al*., 2011; Miao *et al*., 2013; Pan *et al*., 2013; Nosova *et al*., 2015; Chen *et al*., 2021; Li *et al*., 2021)。云杉属的大化石也有较多的报道和研究，但以木材和球果化石居多(Miller *et al*., 1970, 1989; Lepage *et al*., 2001; Denk *et al*., 2005; Afonin *et al*., 2012; Klymiuk *et al*., 2012; Li *et al*., 2013; Miao *et al*., 2013; Brown *et al*., 2014; Akkemik *et al*., 2016; Herrera *et al*., 2016; Cheng *et al*., 2018)。针叶化石相对较少，仅有零星报道(Matsuoka, 1978; Matsumoto *et al*., 1994; Jackson *et al*., 1999; Herrera *et al*., 2016)。由于化石保存状况等原因，该属已知针叶化石的分类鉴定多基于宏观形态，而叶表皮微形态特征的研究较少(Matsuoka, 1978; Matsumoto *et al*., 1994; Jackson *et al*., 1999)，可能影响了其分类鉴定的准确性。尽管云杉属的针叶在宏观形态特征上可以不同程度地与松科其他属相区别，包括其四棱的叶形、无叶柄、上下表面中脉均隆起等，但叶表面微形态研究无疑增加了属下分类鉴定的可能性。

最近，笔者及团队在地处青藏高原东南缘的云南保山盆地的新近纪羊邑组中发现了一批三维立体保存的针叶化石，并从中识别出了大量的云杉属针叶化石。本研究通过对这些针叶化石的宏观形态学和微形态学研究，以及其与现生材料的详细对比，确定化石的最近现生亲缘种(Nearest Living Relative, NLR)。同时，本文基于最近现生亲缘种在青藏高原东南缘的现代海拔分布，讨论盆地当时的海拔高度，为青藏高原东南缘的海拔演变历史提供新的化石证据。

2　化石产地与地质年代

保山盆地地处云南西部，属青藏高原东南缘的南部(图1)。保山盆地呈南北走向，长33 km，宽7–10 km。保山盆地是新生代中晚期形成的断陷盆地，盆地发育新近纪羊邑组，厚300–700 m，主要由青灰色黏土粉砂岩和灰褐色-灰黄色泥质粉砂岩

组成, 其间夹褐煤层(云南省地质矿产局, 1990; 戈鸿儒和李代芸, 1999)。本研究的化石产自盆地东南角的羊邑镇干沟煤矿, 化石所在层位属羊邑组的上部, 岩性为灰褐色-灰黄色泥岩, 其间夹杂一碳质粉砂岩薄层, 产大量植物碎屑。之前的地层和生物地层对比认为, 羊邑组的地质年代为晚上新世(戈鸿儒和李代芸, 1999), 之后的多项古植物和孢粉研究均采用了这一定年结果(徐景先等, 2003; 肖良等, 2006; 李娜等, 2009; Xu *et al*., 2004; He *et al*., 2014)。然而, 古地磁测年显示, 保山盆地新近纪地层的年代跨度约为8.0–3.0 Ma (蒲宗文等, 2018)。最近, 干沟煤矿附近的清水沟煤矿的古地磁研究显示, 其最顶部煤层的地质年代约为6.0 Ma (Li *et al*., 2020)。由于该煤层与干沟煤矿最顶层的煤层为同一沉积年代(Li *et al*., 2020), 而本研究的化石层位又位于煤层的上方(图1), 因此, 可以确定化石层的地质年代为最晚中新世至上新世。

3 材料与方法

3.1 针叶化石的处理与研究

从化石点采集了大量的含植物碎屑的碳质沉积物, 并在实验室筛选获得了400余份针叶化石, 大部分为不完整的片段。借助超声波清洗仪(GT-1620QTS), 在温和模式下对这些针叶化石进行震动清洗, 去除附着在其表面的细小颗粒物。阴干后, 将化石移至体视显微镜下观察, 初步识别出了380份的云杉属针叶化石。首先, 将这些针叶化石移至超景深体视显微镜(Zeiss Smart zoom 5)下观察, 重点观察叶尖、叶基及上、下表面等特征, 并拍照。接着, 挑选一些保存较好的化石标本, 借助扫描电子显微镜(Scanning Electronic Microscope, SEM; Zeiss EVO LS10)进一步研究叶片表面微形态。为了同时扫描同一针叶化石的上、下表面, 我们将一个化石标本分成两段, 分别将其中一段的上表面和另一段的下表面朝上置于贴有导电胶的钉形样品台上, 喷金后进行电镜扫描, 重点观察气孔带、气孔线、气孔和非气孔带的表皮细胞。

3.2 现生对比材料的处理与研究

为了准确鉴定化石, 我们选取云杉属6个现生种的针叶与化石进行形态对比, 这6个种包括云杉(*Picea asperata* Mast.)、油麦吊云杉(*Picea brachytyla* var. *complanata* (Mast.) W. C. Cheng ex Rehder)、丽江云杉(*Picea likiangensis* (Franch.) E. Pritz.)、紫果云杉(*Picea purpurea* Mast.)、鳞皮云杉(*Picea retroflexa* Mast.)和青杄(*Picea wilsonii* Mast.), 6个现生种均分布于青藏高原东南缘, 覆盖

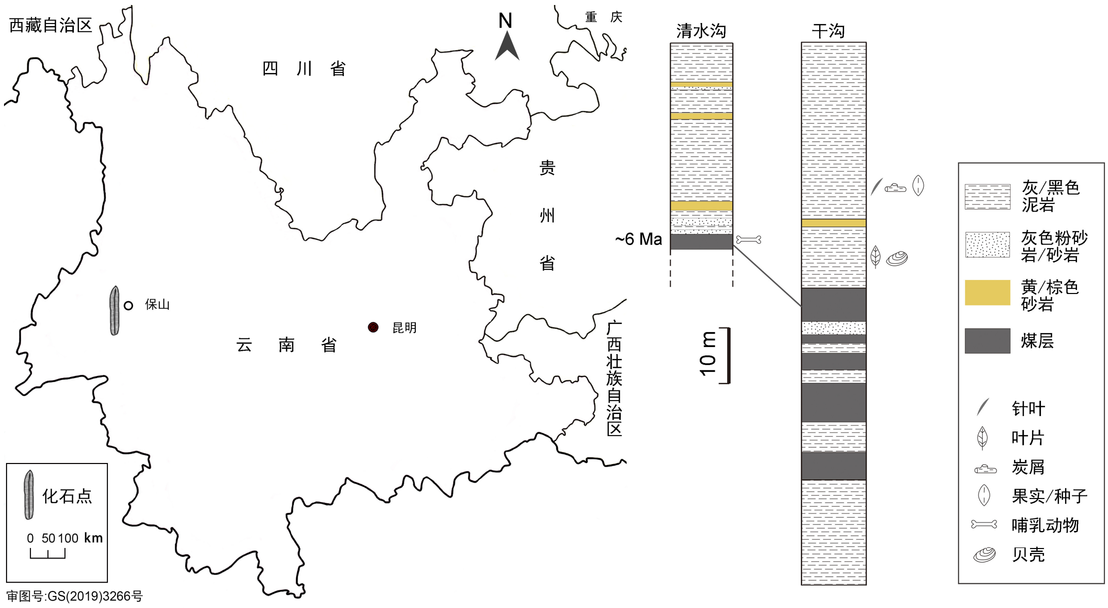

图 1 化石产地的地理位置与地层序列

Fig. 1 Geographic location and geological setting of the fossil site

该地区云杉属的所有物种，同时，占我国该属物种的约50%。现生对比材料(针叶)全部来自中国科学院昆明植物研究所(KUN)标本馆的馆藏标本。首先，我们将现生针叶在清水中浸泡30分钟，然后用小毛刷轻轻地刷洗针叶表面，从而去除附着于表面的细小颗粒物。接着将针叶转至75%的乙醇溶液中静置3–5分钟，并用小毛刷重复刷洗表面，进一步去除表面的附着物。阴干后，将针叶置于氯仿($CHCL_3$)中静置30秒，用小毛刷轻轻刷洗针叶表面，随后将针叶再次放入75%的乙醇溶液中静置2分钟，取出并阴干。如此反复操作，直至在体视显微镜下基本观察不到覆盖在气孔带上的白色物质为止。最后，将针叶移至超景深体视显微镜下观察，主要观察叶尖、叶基及上、下表面等特征。同时，我们从每个现生种选取一枚针叶，进一步借助扫描电子显微镜观察。如同针叶化石的扫描，我们将针叶中间部分剪成两段，分别将其中一段的上表面和另一段的下表面朝上置于贴有导电胶的钉形样品台上，喷金后进行电镜扫描，重点观察气孔带、气孔线、气孔和非气孔带的表皮细胞。

4　系统古生物学

松科　Pinaceae

云杉属　*Picea* A. Dietrich

似油麦吊云杉　*Picea brachytyla* var. *complanata* (Mast.) W. C. Cheng ex Rehder

化石材料　380份针叶化石，大部分为不完整的针叶片段。

化石产地　云南保山盆地东南面的羊邑镇干沟煤矿(24°58′54″N, 99°14′12″E)。

地层与地质年代　羊邑组，最晚中新世至上新世。

化石保存地　中国科学院昆明植物研究所(KUN)东亚植物多样性与生物地理学重点实验室。

标本号　YYGG-001–YYGG-380。

描述　针叶长条形，扁平，仅叶基处呈四棱形(图2, 4-A, 4-D)；叶尖多急尖，少渐尖(图2-A, 2-B, 3-A, 3-D)，叶基截形，无叶柄(图2-A, 2-C, 4-A, 4-D)；上、下表面的中脉均显著隆起(图2-B, 2-C)；气孔上生型；上表面有2个气孔带，分居中脉两侧，

图2　超景深体视显微镜下的云杉属针叶化石

Fig. 2　Images of fossil *Picea* leaves taken under an ultra-depth three-dimensional microscope

A. 完整针叶的化石，示上表面(**A1**)和下表面(**A2**)，标本号: YYGG 002; **B**. 不完整针叶的化石，示近叶尖部分的上表面(**B1**)和下表面(**B2**)及隆起的中脉，标本号: YYGG 005; **C**. 不完整针叶的化石，示近叶基部分的上表面(**C1**)和下表面(**C2**)及隆起的中脉，标本号: YYGG 021。比例尺为1 mm。

A. Intact fossil leaf, showing adaxial (**A1**) and abaxial (**A2**) surfaces, speciment No. YYGG 002; **B**. Fragmentary fossil leaf, showing the adaxial (**B1**) and abaxial (**B2**) surfaces of the apical part, both with a raised midvein, YYGG 005; **C**. Fragmentary fossil leaf, showing adaxial (**C1**) and abaxial (**C2**) surfaces of the basal part, both with a raised midvein, YYGG 021. Scale bars = 1 mm.

每个气孔带具5–6条气孔线(图3-A, 4-A, 5-A), 气孔线间距均匀, 气孔线中的气孔大部分连续分布, 少部分不连续分布(图3-B, 4-B, 5-B); 气孔椭圆形至长椭圆形, 偶长方形, 有或无气孔塞(图3-B, 4-B, 5-B); 保卫细胞长椭圆形至哑铃型, 细胞壁光滑, 副卫细胞不清晰(图3-B, 4-B, 5-B); 气孔带的其他表皮细胞及非气孔带的表皮细胞不清晰; 下表面无气孔, 表皮细胞矩形, 排列紧密, 细胞壁波浪状弯曲(图3-E, 3-F, 4-E, 4-F, 5-E, 5-F)。

5 讨 论

5.1 形态对比

松科植物的属间分类主要根据其形态多样的球果、种鳞、花粉等器官与结构(Schmidt, 1989; Fu *et al*., 1999; Farjon, 2001)。然而, 其针叶亦具有多样的形态特征。已有的针叶宏观形态与微形态研究显示, 松科各属之间在针叶的总体形态上存在显著差异, 如形状具有针形、条形、四棱状条形等(姚壁君等, 1982; Liu, 1982; 吴瀚, 1984; 中国科学院昆明植物研究所, 1986; 傅立国等, 2000; 邵邻相等, 2005; 王岩, 2008; Miranda and Chaphekar, 1980; Fu *et al*., 1999; Kim *et al*., 1999; Whang *et al*., 2001, 2004; Ghimire *et al*., 2015)。因此, 仅依据针叶便具有松科属间分类的可能性。我们基于这些研究及对馆藏标本的观察, 总结出了松科在针叶宏观形态与微形态上的属间差异。如表1所示, 大部分属的针叶在叶基均有变窄的趋势, 包括冷杉属、铁杉属、银杉属、黄杉属、落叶松属、金钱松属、油杉属和雪松属, 只有云杉属和松属的针叶近叶基时没有显著的大小变化, 且两者均缺少叶柄。我们的针叶化石基部截形, 无叶柄, 可以与云杉属和松属作进一步对比。云杉属的针叶边缘平滑, 而松属的针叶边缘具有排列整齐的刚毛(Whang *et al*., 2001, 2004), 两者因此可以相区分。尽管在化石的保存过程中, 松属针叶的刚毛容易发生脱落,

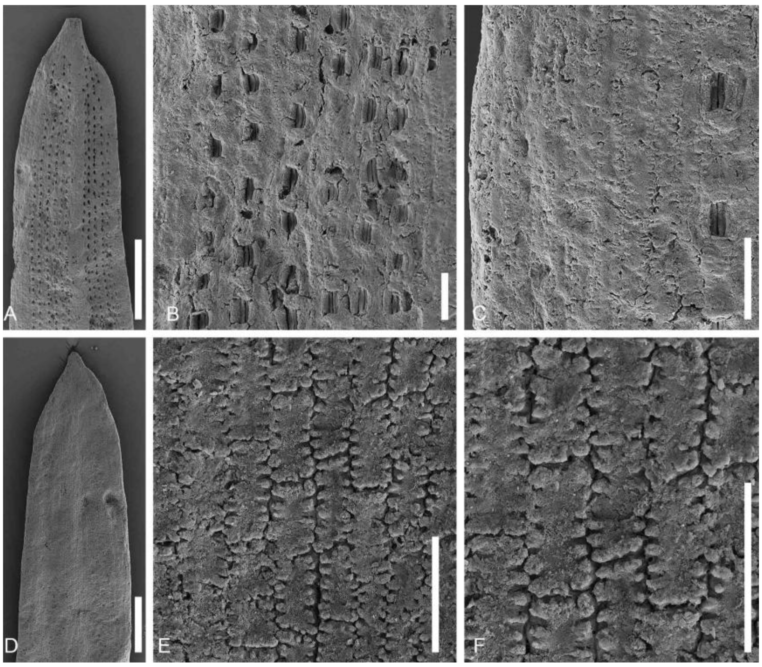

图3 电镜下针叶化石近叶尖部分的表面微形态

Fig. 3 SEM images showing microscopic surface features of the apical part of fossil *Picea* leaves

A–**C**. 上表面, 标本号: YYGG 006; **A**. 总体形态, 示叶尖, 隆起的中脉及中脉两侧的气孔带; **B**. 气孔带, 示6条气孔线; **C**. 非气孔区, 示普通表皮细胞及其波浪状的细胞边缘; **D**–**F**. 下表面, 标本号: YYGG 007; **D**. 总体形态, 示叶尖, 平滑的表面及隆起的中脉. **E**–**F**. 表面放大, 示矩形的表皮细胞及波浪状的细胞边缘。比例尺为 0.5 mm (A, D), 50 μm (B, C, E, F)。

A–**C**. Adaxial surface, speciment No. YYGG 006; **A**. General view showing acute apex, raised midvein and stomatal bands on both sides of the midvein; **B**. Stomatal band with six stomatal files; **C**. Non-stomatal area; epidermal cells not obvious. **D**–**F**. Abaxial surface, speciment No. YYGG 007; **D**. General view showing acute apex, smooth surface and weakly raised midvein; **E**, **F**. Close-up of the abaxial surface, showing rectangular epidermal cells with undulate anticlinal walls. Scale bars = 0.5 mm (A, D), 50 μm (B, C, E, F).

但留下的排列整齐的圆形痕迹仍然清晰可见，是判断松属针叶化石的重要特征。例如，之前发现于云南兰坪盆地上新世三营组的华山松(*Pinus armandii* Franch.)针叶化石在扫描电子显微镜下可清楚地观察到刚毛脱落的痕迹(Huang *et al*., 2020)。我们的针叶化石为扁平形，且不具刚毛，扫描电子显微镜下也未观察到刚毛脱落的痕迹，可以排除其为松属的可能性。因此，我们将当前化石定为云杉属。针叶化石的其他形态学特征也进一步支持了这一属级界定。例如，当前化石上、下表面的中脉均有隆起，与云杉属的针叶相符，而与冷杉属、铁杉属和黄杉属等属的针叶仅下表面中脉隆起，

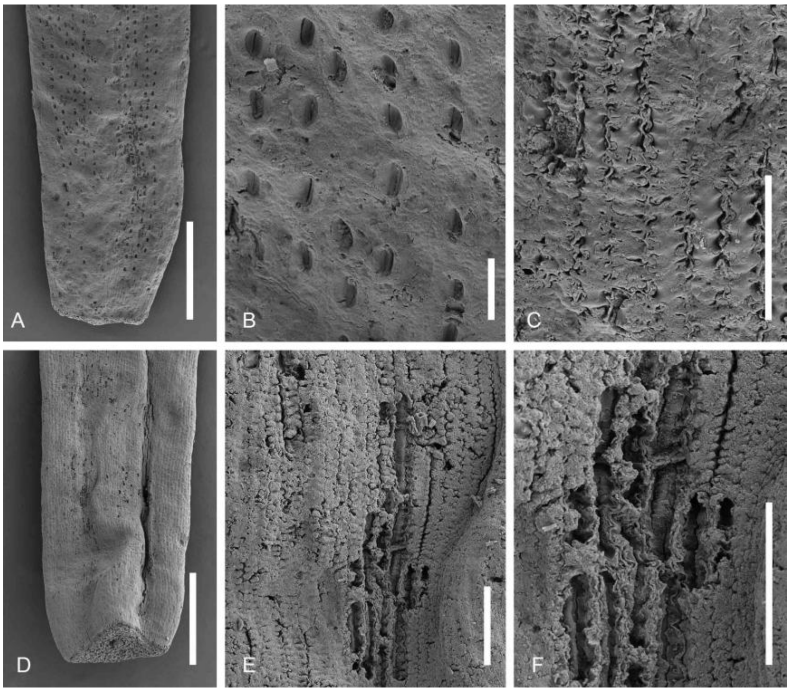

图 4　电镜下针叶化石近叶基部分的表面微形态

Fig. 4　SEM images of microscopic surface features of the basal part of fossil *Picea* leaves

A–C. 上表面，标本号: YYGG 020; **A**. 总体形态，示棱形，截形的叶基，隆起的中脉及中脉两侧的气孔带; **B**. 气孔带，示 5 条气孔线及椭圆形气孔; **C**. 非气孔带的表皮细胞及波浪状细胞边缘; **D–F**. 下表面，标本号: YYGG 023; **D**. 总体形态，示棱形，截形的叶基及隆起的中脉; **E–F**. 表面放大，示长矩形的表皮细胞及波浪状的细胞边缘。比例尺为 0.5 mm (A, D), 50 μm (B, C, E, F)。

A–C. Adaxial surface, speciment No. YYGG 020; **A**. General view showing prismatic, truncate base, raised midvein and stomatal bands on both sides of the midvein; **B**. Stomatal band with five stomatal files; **C**. Close-up of the non-stomatal area, showing rectangular epidermal cells with undulate anticlinal walls; **D–F**. Abaxial surface, speciment No. YYGG 023; **D**. General view showing prismatic, truncate base and raised midvein; **E–F**. Close-up of the abaxial surface, showing elongated rectangular epidermal cells with undulate anticlinal walls. Scale bars = 0.5 mm (A, D), 50 μm (B, C, E, F).

表 1　松科 10 属的针叶形态对比

Table 1　Leaf morphology of 10 genera in Pinaceae

属	叶形	叶尖	叶基	叶柄	中脉	刚毛
油杉属	条形	尖形	变窄	有	下表面隆起	无
冷杉属	条形	尖形、圆形、凹形	变窄	无或不显著	下表面隆起	无
黄杉属	条形	尖形、凹形	变窄	有	下表面隆起	无
铁杉属	条形	尖形、圆形、凹形	变窄	有	下表面隆起	有或无
银杉属	条形	尖形、圆形	变窄	有	下表面隆起	无
云杉属	条形、四棱形	尖形	无明显变窄	无	上、下表面隆起	无
落叶松属	条形	尖形	变窄	无或不显著	无显著隆起	无
金钱松属	条形	尖形	变窄	无或不显著	无显著隆起	无
雪松属	针形	尖形	变窄	无	无显著中脉	无
松属	针形	尖形	无明显变窄	无	无显著中脉	有

而上表面中脉凹陷的特征不符；化石的叶尖为尖形，与云杉属的针叶相符，而与冷杉属、铁杉属、黄杉属等的针叶存在叶尖圆形或凹形的特征不符。

为了化石的属下分类鉴定，找出化石可能的最近现生亲缘种，我们基于已有的文献资料(中国科学院中国植物志编辑委员会，1978；中国科学院昆明植物研究所，1986；傅立国等，2000)及对馆藏标本的观察，归纳总结了6个主要分布于青藏高原东南缘的云杉属现生种针叶的宏观形态和微形态特征(表2)。并将针叶化石与这6个现生种的针叶进行了宏观形态和微形态对比。对比发现，这些云杉属现生种的针叶形态可以分为两类：四棱形和条形(扁平形)，前者包括云杉、鳞皮云杉和青杆，后者仅有1种，即油麦吊云杉，而丽江云杉和紫果云杉则介于两者之间。除了总体形态，两种类型的针叶在气孔分布上也大不相同：四棱形针叶四面具气孔，而扁平形针叶只有上表面具气孔，下表面仅在近叶尖处偶见少数气孔分布。我们的化石扁平形，但由于化石保存过程中的挤压作用，四棱形针叶也可能变成扁平形针叶，因此，不足以证明

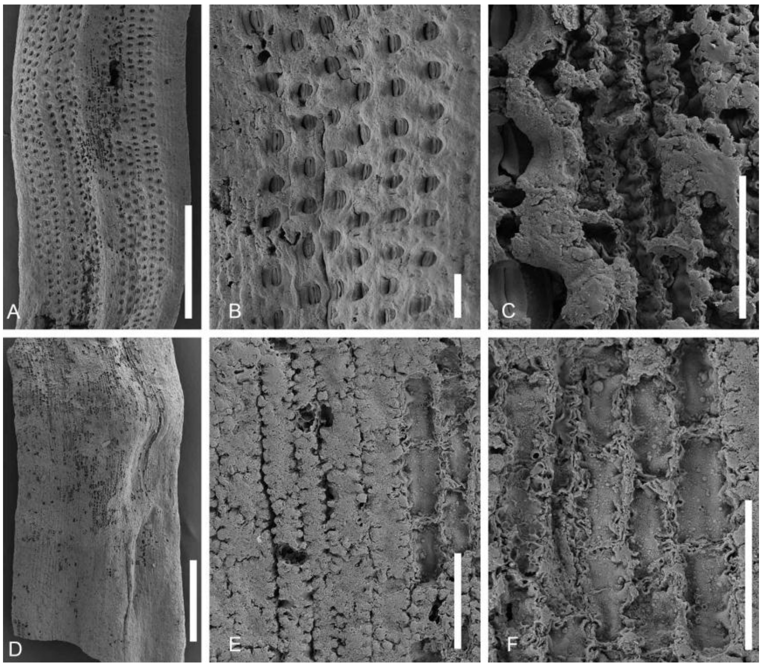

图5 电镜下针叶化石近叶中部分的表面微形态

Fig. 5 SEM images of microscopic surface features of the middle part of a fossil *Picea* leaf

A–C. 上表面，标本号: YYGG 080; **A**. 总体形态，示扁平的叶形，隆起的中脉及中脉两侧的气孔带; **B**. 气孔带，示6条气孔线; **C**. 非气孔带的表皮细胞及波浪状细胞边缘; **D–F**. 下表面，标本号: YYGG 081; **D**. 总体形态，示扁平的叶形，无气孔的表面及略微隆起的中脉. **E–F**. 表面放大，示矩形的表皮细胞及波浪状的细胞边缘。比例尺为 0.5 mm (A, D), 50 μm (B, C, E, F)。

A–C. Adaxial surface, speciment No. YYGG 080; **A**. General view showing flattened leaf with raised midvein and stomatal bands on both sides of the midvein; **B**. Stomatal zone with six stomatal files; **C**. Close-up of non-stomatal area, showing rectangular epidermal cells with undulate anticlinal walls; **D–F**. Abaxial surface of YYGG 081; **D**. General view showing flattened leaf with non-stomatal area and slightly raised midvein; **E–F**. Close-up of the abaxial surface, showing rectangular surface cells with undulate anticlinal walls. Scale bars = 0.5 mm (A, D), 50 μm (B, C, E, F).

表2 云杉属现生种的针叶形态与微形态

Table 2 Leaf morphology and micromorphology of extant *Picea*

种	叶形	叶尖	上表面气孔分布	下表面气孔分布
云杉	四棱形	渐尖或急尖	中脉两侧各有4–8条气孔线	中脉两侧各有4–6条气孔线
油麦吊云杉	条形	渐尖或急尖	中脉两侧各有5–7条气孔线	无气孔
丽江云杉	条形至四棱形	渐尖或急尖	中脉两侧各有4–7条气孔线	有1–2条气孔线，稀无气孔线
紫果云杉	条形至四棱形	渐尖或急尖	中脉两侧各有2–3条气孔线	无气孔，偶见1–2条不完整的气孔线
鳞皮云杉	四棱形	渐尖或急尖	中脉两侧各有6–7条气孔线	中脉两侧各有4–5条气孔线
青杆	四棱形	渐尖	中脉两侧各有4–6条气孔线	中脉两侧各有4–6条气孔线

其代表四棱形还是扁平形针叶。然而, 由于化石仅一面有气孔, 不符合云杉属四棱形针叶的特征, 从而确定其属于扁平形针叶类型。因此, 我们将化石与具有扁平形针叶的 3 个种, 即丽江云杉、油麦吊云杉和紫果云杉作进一步对比(图 6)。

如表2所示, 紫果云杉的针叶上表面气孔线较少, 中脉两侧的每个气孔带均只有2–3条气孔线, 明显少于针叶化石的5–6条气孔线; 此外, 紫果云杉的针叶有时候在下表面也出现1–2条不完整的气孔线, 而针叶化石的下表面未见有气孔线分布。因此, 化石不可能属于紫果云杉。丽江云杉的针叶上表面的每个气孔带有4–7条气孔线, 气孔线间隔均匀, 气孔线上的气孔常连续分布, 个别间断分布, 下表面无气孔或偶尔出现1–2条不连续的气孔, 与化石更相符, 但仍然存在一些细微差异。油麦吊云杉的针叶上表面的每个气孔带有5–7条气孔线, 气孔线间隔均匀, 气孔线上的气孔常连续分布, 偶间断分布, 下表面无气孔(图7), 与化石最为吻合。然而, 在缺少其他器官结构(木材、球果和花粉)的情况下, 很难确定化石是否真正代表了油麦吊云杉, 故我们将其暂定为油麦吊云杉的相似种, 即似油麦吊云杉。

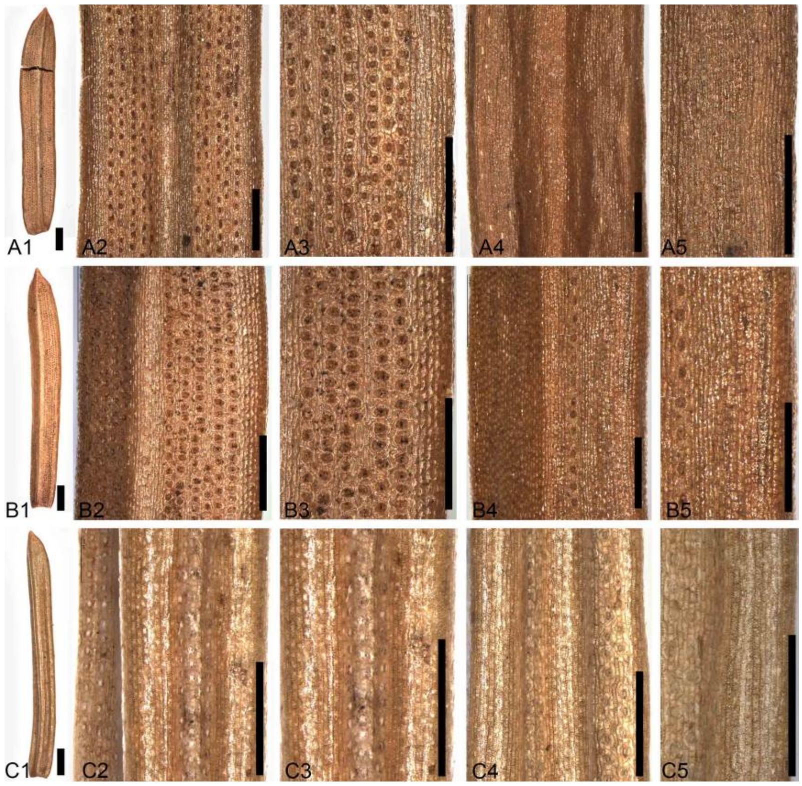

图 6 现生云杉属的针叶及其上、下表面特征

Fig. 6 Extant *Picea* leaves and their adaxial and abaxial epidermal characters

A. 油麦吊云杉; **A1**. 针叶总体形态: 扁平, 叶尖急尖, 叶基截形, 无叶柄; **A2**, **A3**. 上表面, 中脉隆起, 两侧具气孔带, 每个气孔带多6条气孔线, 偶5条或7条气孔线; **A4**, **A5**.下表面, 无气孔, 中脉隆起; **B**. 丽江云杉; **B1**. 针叶总体形态: 扁平, 叶尖急尖, 叶基截形, 无叶柄; **B2**, **B3**. 上表面, 中脉隆起, 两侧具气孔带, 每个气孔带多5条气孔线, 偶4条或6条气孔线; **B4**, **B5**. 下表面, 有1–2条不连续的气孔线, 中脉隆起; **C**. 紫果云杉; **C1**. 针叶总体形态: 扁平, 叶尖渐尖, 叶基截形, 无叶柄; **C2**, **C3**. 上表面, 中脉隆起, 两侧具气孔带, 每个气孔带多3条气孔线, 偶2条或4条气孔线; **C4**, **C5**. 下表面, 有1–2条不连续的气孔线, 中脉隆起。比例尺为1 mm (A1, B1, C1), 0.5 mm (A2, A3, B2, B3, C2, C3)。

A. *Picea brachytyla* var. *complanata*; **A1**. General shape, showing flattened leaf with acuminate apex, and truncate base without a petiole; **A2**, **A3**. Adaxial surface with raised midvein and stomatal bands on both sides of the midvein; each stomatal band is composed of six, sometimes five or seven stomatal files; **A4**, **A5**. Abaxial surface with slightly raised midvein and no stomata; **B**. *Picea likiangensis*; **B1**. General shape, showing flattened leaf with acuminate apex, and truncate base without a petiole; **B2**, **B3**. Adaxial surface with raised midvein and stomatal bands on both sides of the midvein; each stomatal band is composed of five, sometimes four or six stomatal files; **B4**, **B5**. Abaxial surface with slightly raised midvein and 1–2 discontinuous stomatal files; **C**. *Picea purpurea*; **C1**. General shape, showing the slightly flattened leaf with acuminate, and truncate base without a petiole; **C2**, **C3**. Adaxial surface with raised midvein and stomatal bands on both sides of the midvein; each stomatal band is composed of three, sometimes two or four stomatal files; **C4**, **C5**. Abaxial surface with raised midvein and 1–2 discontinuous stomatal files. Scale bars = 1 mm (A1, B1, C1), 0.5 mm (A2, A3, B2, B3, C2, C3).

5.2 古海拔指示意义

云杉属植物喜低温，主要分布于北半球高纬度或高海拔地区(中国科学院中国植物志编辑委员会, 1978; 吴征镒, 1980; Farjon, 2001; 刘增力等, 2002; Fan *et al*., 2009; Miao *et al*., 2022)。青藏高原东南缘由于纬度相对较低,云杉属植物仅分布于海拔相对较高的地区(刘增力等, 2002; Fan *et al*., 2009)。因此，该地区云杉属化石的发现，对揭示地质时期的海拔情况具有重要意义。由于云杉属的海拔分布受纬度影响较大，纬度越高，其分布的海拔越低，为了减少纬度对古海拔推测的影响，我们仅依据化石点所在的青藏高原东南缘的云杉属现代海拔分布，来推测化石点在地质时期的海拔高度。青藏高原东南缘现有云杉属植物6种，分别为云杉、油麦吊云杉、丽江云杉、紫果云杉、鳞皮云杉和青杆。根据《横断山区维管植物》记载，这6个种均分布于该地区的中高海拔(表3，图8)，其中海拔分布最低的是油麦吊云杉，为2000–3600 m; 海拔分布最高的是紫果云

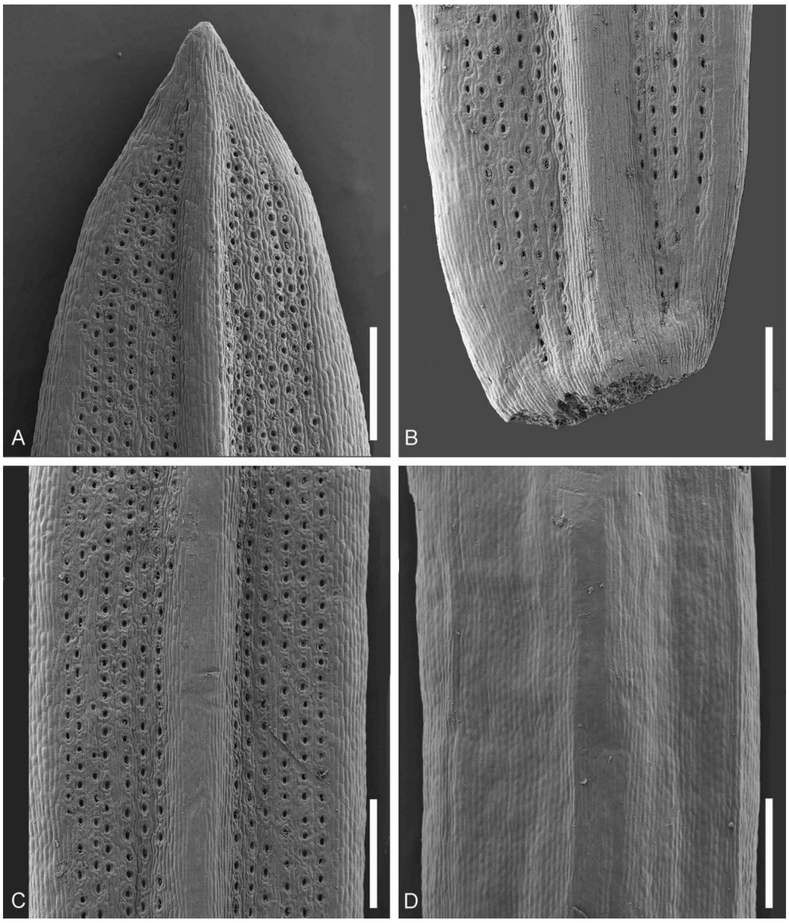

图7 电镜下油麦吊云杉现生针叶的表面微形态

Fig. 7 SEM images of microscopic leaf epidermal characters of *Picea brachytyla* var. *complanate*

A. 叶尖部分的上表面，中脉隆起; B. 叶基部分的上表面，中脉隆起; **C**. 叶中部分的上表面，中脉隆起，两侧具气孔线，每个气孔带6条气孔线; **D**. 叶中部分的下表面，无气孔，中脉隆起。比例尺为0.5 mm。

A. Adaxial surface near the apex, with raised midvein; **B**. Basal adaxial surface with raised midvein and truncate base without a petiole; **C**. Middle adaxial surface with raised midvein and stomatal bands on both sides of the midrib; each stomatal band comprising six or seven stomatal files; **D**. Middle abaxial surface with slightly raised midvein and no stomata. Scale bars = 0.5 mm.

表3 青藏高原东南缘云杉属现生种的海拔分布范围(王文采, 1993)

Table 3 Altitudinal ranges of extant *Picea* species at the southeastern margin of the Tibetan Plateau (Wang, 1993)

种	云杉	油麦吊云杉	丽江云杉	紫果云杉	鳞皮云杉	青杆
海拔(m)	2400–3600	2000–3600	2300–4000	2600–4000	2100–4000	2400–2800

杉, 为2600–4000 m。属下分类鉴定显示, 我们的化石与油麦吊云杉最为接近, 根据其现代海拔分布, 本文推测, 最晚中新世至上新世时期, 保山盆地羊邑地区的海拔可能为2000–3600 m。考虑到新近纪全球温度普遍高于现在(Zachos *et al*., 2001; Zachos *et al*. 2008; Pagani *et al*., 2010; Goldner *et al*., 2014; Burke *et al*., 2018), 该化石很可能比其现生近缘种具有更高的海拔分布, 从而推测, 羊邑地区当时的海拔可能不低于2000–3600 m这一海拔范围。之前的孢粉记录显示, 自上新世以来, 保山盆地或其附近地区一直有云杉属植物的分布(徐景先等, 2003; Xu *et al*., 2004), 可能同样显示了当时较高的海拔高度; 之前的植物大化石研究显示, 羊邑地区在上新世时期分布有丰富的高山栎组(*Quercus* sect. *Heterobalanus*)植物(肖良等, 2006; He *et al*., 2014), 由于高山栎组植物现今主要生长于青藏高原东南缘的中高海拔地区, 因此也反映了当时较高的海拔。这些研究结果进一步支持了我们关于羊邑地区的古海拔推测。地质时期, 青藏高原东南缘经历了剧烈的抬升, 其中北面地区抬升较早, 始于始新世, 抬升程度也较大, 诸多地方抬升了3000 m以上(Li *et al*., 2015; Tang *et al*., 2017; Li *et al*., 2018; Su *et al*., 2019; Xiong *et al*., 2020); 南面地区抬升较晚, 主要开始于中新世, 且抬升程度较低(王成善等, 2009; Clark *et al*., 2005; Hoke *et al*., 2014; Gourbe *et al*., 2017; Zhang *et al*., 2019)。保山盆地位于青藏高原东南缘的南面, 我们的古海拔推测表明, 其至少在最晚中新世至上新世时期就已经抬升到了相当高的海拔高度, 进一步丰富了青藏高原东南缘的海拔抬升历史, 尤其显示了其南面地区的抬升过程。现在, 保山盆地羊邑地区的海拔约为1650 m, 明显低于我们推测的古海拔, 暗示了该地区自最晚中新世至上新世以来可能经历了海拔降低的过程。导致这种海拔降低可能是地壳构造活动, 或地表过程, 或两者共同作用的结果, 但哪个因素在保山盆地海拔下降中占主导因素, 需今后进一步研究。

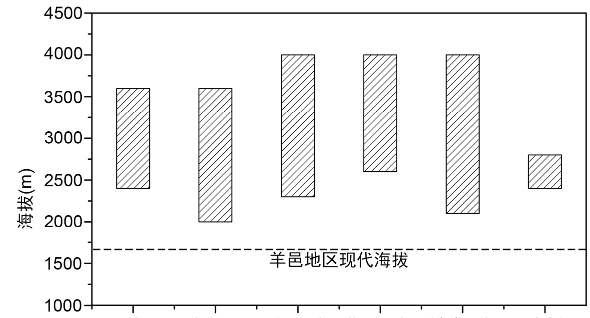

图 8　青藏高原东南缘云杉属现生种的海拔分布及与保山盆地羊邑地区现代海拔的对比

Fig. 8　Altitudinal ranges of extant *Picea* species at the southeastern margin of the Tibetan Plateau and their comparison with the modern altitude at Yangyi of the Baoshan Basin

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