新生代早期鱼类演化的热点区域: 环北部湾陆上盆地 古近纪鱼化石研究成果与展望

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摘要 环北部湾新生代的鱼化石在20世纪曾有过少量研究. 自2002年以来, 本文作者等在广西南宁、南宁、百色、广东茂名、三水及海南文昌等环北部湾陆上盆地的古近纪地层中采到了一批鱼化石, 并对其中一些做了初步的研究. 本文旨在对已有的成果和进展做概览, 为进一步深入研究的导向做些探讨. 总的来说, 本区域古近纪鱼群包括软骨鱼类的鲨鱼类(*Selachii*, *Elasmobranchii*), 硬骨鱼类的骨舌鱼目(*Osteoglossiformes*)、鲱超目(*Clupeomorpha*)、鲤形目(*Cypriniformes*)、鲇形目(*Siluriformes*)和鲈超目(*Percomorpha*)等. 鱼化石数量和种类丰富, 中生代鱼类的典型代表的孑遗类群(埃笠姆鲱目†*Ellimmichthyiformes*)与新生代新兴、分异的主要类群(鲤形目)并存, 几乎涵盖了新生代非海相鱼类所有主要类群的早期代表. 值得注意的是, 本区域且区域内各盆地的鱼群均以鲤形目为主, 是目前世界上古近纪鲤形目化石科一级类群最集中、最丰富的区域. 三水盆地古新统埤心组的江汉鱼科†*Jianghanichthyidae*三水江汉鱼†*Jianghanichthys sanshuiensis*、茂名盆地始新统油柑窝组的鲤科*Cyprinidae*茂名始原鲤†*Eoprocypis maomingensis*、和南宁盆地渐新统邕宁组的鲇科*Cobitidae*南宁鲇†*Cobitis nanningensis*分别是各科最早期的化石记录, 代表着鲤形目主要分支的分异时间和早期形态. 再者, 含鱼化石地层的年代从古新世晚期延续至渐新世, 除鲤形目和骨舌鱼目外的其他几类鱼可生活于海水和淡水, 这几类鱼化石的研究将为判断当时是否存在过海侵提供鱼化石证据, 为研究鱼类区系与环境协同演化提供理想的条件. 综上, 环北部湾陆上盆地无疑是新生代淡水鱼类区系起源与演化的热点区域(evolutionary hotspot), 深入研究本区域古近纪鱼群将为诠释现代鱼类区系的形成、有关类群的起源演化以及与之相关的古动物地理学和古环境提供重要的化石证据.

关键词 环北部湾, 古近纪鱼化石, 演化, 古环境

北部湾(Beibu Gulf, 亦称东京湾 Gulf of Tonkin)位于中国南海的西北部, 是中国大西南地区出海最近的通道. 环北部湾的我国南部及越南北部的陆上

盆地古近纪地层发育, 蕴含有丰富的鲤形目(*Cypriniformes*)、鲇形目(*Siluriformes*)等鱼化石, 这些化石可为追溯现代鱼类的渊源提供重要证据, 亦可

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为含鱼化石地层属陆相或非海相作出判断。然而,以往对这些盆地古近纪鱼类化石的系统采集和研究很少,仅有刘宪亭^[1]研究了产自茂名盆地油柑窝组钻井岩心的一尾鱼化石,以及王将克等人^[2]研究了发现于三水盆地的鱼化石群。随着人们对全球变化,尤其是近现代地质事件对人类社会影响的关注,新生代化石研究也日益受到重视。新千年以来,中国科学院古脊椎动物与古人类研究所(以下简称古脊椎所)和广西壮族自治区自然博物馆(以下简称广西自然博物馆)多次在我国环北部湾陆上盆地古近系进行野外考察、发掘,目前已在广西南明盆地、百色盆地和南宁盆地,广东茂名盆地和三水盆地,以及海南长昌盆地(图1)的古近纪地层中采集到了鲤形目、鲱超目(Clupeomorpha)、鲇形目、骨舌鱼目(Osteoglossiformes)和鲈超目(Percomorpha)等鱼类化石(本文分类主要采用Nelson等人^[3]的分类系统),并对所采到的一些化石做了初步的研究和描述。与此同时,国际同行在与广西南明盆地相邻的越南北部的纳堂盆地和高平盆地开展古生物化石发掘与研究,对古近纪化石做了初步报道^[4,5]。本文旨在对本区域古近纪鱼类研究做一阶段性总结,为进一步深入研究的导向做

些探讨。

1 研究区域及含鱼化石地层概况

环北部湾的粤桂琼地区分布着一系列陆上新世代沉积盆地,其中一些已采集到古近纪鱼类化石,如广西的宁明盆地、百色盆地和南宁盆地,广东的茂名盆地和三水盆地,以及海南的长昌盆地。这几个盆地在中国古近系和新近系地层区划上均归属岭南地层区^[6,7]。其中,宁明盆地是一沿NEE向大断裂分布的断陷盆地,位于广西西南部宁明县北回归线以南,与越南境内的纳堂盆地几乎相连。该盆地沉积有一套河湖相的古近纪地层,沉积总厚度达1490 m,前人曾在其中的渐新统宁明组(相当于邕宁群第二段中上部)采到鱼化石,并将它归入鲤科(Cyprinidae)鲃属(*Barbus*),但没有描述和图版^[8,9]。2002年始,广西自然博物馆与古脊椎所等单位多次在该盆地野外工作,系统采集宁明组的化石,目前采集到的标本有丰富的鱼类和植物大化石,以及少量的昆虫化石^[10~21]。鱼化石群以鲤形目鲤科为主,其次是鲱超目的埃笠姆鲱目(†*Ellimmichthyiformes*)(化石类群在名称前加“†”作标记,下同),有少量的鲇形目及鲈超目的鰕

图1 环北部湾古近纪鱼化石主要地点(红三角)。1, 三水盆地; 2, 茂名盆地; 3, 长昌盆地; 4, 南宁盆地; 5, 百色盆地; 6, 宁明盆地; 7, 越南纳堂盆地; 8, 高平盆地。底图下载自国家测绘地理信息局网站, <http://bzdt.nasg.gov.cn/>

Figure 1 Main localities of Palaeogene fishes from the onshore basins around Bohai Gulf (red triangle) (Based on the map downloaded from <http://bzdt.nasg.gov.cn/>). 1, Sanshui Basin; 2, Maoming Basin; 3, Changchang Basin; 4, Nanning Basin; 5, Baise Basin; 6, Ningming Basin, China; 7, Na Duong Basin and 8, Cao Bang Basin, Vietnam

虎鱼目(Gobiiformes)鱼类。

南宁盆地是一个NE向延伸的断陷盆地。盆地中第三纪沉积总厚度1800~2400 m, 其中始新统邕江组 and 渐新统邕宁组含有煤层, 产孢粉、介形类、腹足类、双壳类^[9]、鱼和植物大化石^[22]。邕宁组还产哺乳动物化石^[23]。在我们之前, 几乎没有人研究过南宁古近纪的鱼化石。近年来, 广西自然博物馆在该盆地邕宁组采集到了一批鱼骨片和鲤科咽齿化石, 以及龟鳖类骨片及鳄类牙齿。鱼群以鲤形目为主, 有鲤科和鳅科(Cobitidae), 其次是鲇形目, 鲱超目较少^[24]。孢粉分析认为含鱼化石层的时代是渐新世早-中期, 略晚于宁明盆地宁明组含鱼化石层(渐新世早期)^[25]。

百色盆地呈NW—SE向长条状, 古近系总厚度约1500 m^[9], 富含哺乳动物化石, 始新世洞均组还有鲤科“青鱼”(Mylopharyngodon sp.)咽齿^[26](青鱼咽齿臼齿型, 齿面光滑, 与鲤属(Cyprinus)咽齿主行第一枚相似, 仅凭单颗齿不易确定)。丁素因等人^[26]将洞均组划归晚始新世, 但童永生等人^[27]及李茜等人^[28]认为洞均组之上的那读组至少有一部分为中始新世。根据线索, 2017年广西自然博物馆做了两天的野外工作, 采集到一些零散鱼骨片化石。

茂名盆地为一NW向的不对称向斜盆地, 古近纪地层发育, 其中油柑窝组的油页岩层中富含化石, 有植物、螺、蚌、鱼^[1]、爬行动物^[29,30]和哺乳动物化石^[31]。油柑窝组的时代, 基于陆龟科化石^[29,30]及哺乳动物化石^[31]的研究均认为是晚始新世。该盆地的鱼化石, 除了刘宪亭^[1]研究的一尾产自油柑窝组钻井岩芯中的鲤科鱼化石外, 还有茂名石油公司于二十世纪六七十年代发现的软骨鱼纲鲨鱼类(Selachii)的牙齿化石。近年来, 古脊椎所在该盆地油柑窝组新采集到一批包括鲤科^[32]和鲇形目在内的鱼化石。

三水盆地为一NNE向展布的断陷盆地, 古近纪地层发育良好, 化石丰富, 有介形虫、螺、鱼、鸟、哺乳动物等^[33-36]。鱼化石主要产于古新统埤心组-下始新统华涌组, 以埤心组尤为丰富^[2,34]。王将克等人^[2]认为埤心组的鱼化石以鲤科为主, 还有鲇形目鮠科(Bagridae)和鲈形目(Perciformes)鲈科(Serranidae), 其上覆地层西埤组(宝月组)和华涌组也产鲤科化石。但是, 王将克等人^[2]所描述的鲤科化石, 从描述和图版看并无可靠的鲤科鱼类特征^[37,38]。近年, 古脊椎所在该盆地新采集了一批标本, 对其中所谓的纹唇鱼(骨唇鱼)属(“Osteochilus”)化石的研究显示, 它们很可能为鲤形目

唯一化石科——江汉鱼科(†Jianghanichthyidae)鱼类^[39]。在上述新采集标本中还发现了骨舌鱼类化石, 这是该类化石在本区的首次发现。

长昌盆地位于海南岛北部的琼山县境内, 古近纪地层发育, 可分为古新统昌头组和始新统长昌组及瓦窑组。长昌组上段为含煤段, 产丰富的孢粉和植物大化石^[40], 以及腹足类、双壳类和鱼类化石^[41]。根据孢粉组合特征, 雷亦振等人^[42]认为长昌组上段的时代为早始新世晚期—晚始新世早期; Spicer等人^[43]根据植物化石组合认为长昌组的地质时代是中始新世。古脊椎所近年在长昌组采到了一些鲤科化石。化石有待研究。

2 鱼化石研究进展及其研究意义

根据前人研究^[1,2]及笔者等近10多年来采集到的标本(表1), 本区域古近纪鱼类以鲤形目最为丰富, 在各盆地都有分布, 且占多数, 这与本区现代鱼类区系以鲤形目占绝大多数的情形相一致。但其中时代较早的三水盆地的鲤形目化石均属已灭绝的江汉鱼科, 不同于其他盆地的鱼化石群及现代淡水鱼群均以鲤科为主的特点。鲱超目在宁明盆地较为常见, 在南宁盆地有少量发现。除了长昌盆地和百色盆地, 鲇形目在几个盆地都有发现。鲈超目见于三水盆地和宁明盆地, 但三水的是特化等级较低的鲈形目鱼类, 宁明的则属于较特化的鰕虎鱼目。在茂名盆地还有鲨鱼牙齿化石。在三水盆地新发现了骨舌鱼类化石。

表1 环北部湾陆上盆地古近纪主要鱼类及其分布^{a)}

Table 1 Palaeogene fishes and their distribution in basins around Beibu Gulf

	宁明	南宁	百色	三水	茂名	长昌
鲨鱼类	—	—	—	—	+	—
骨舌鱼目	—	—	—	+	—	—
鲱超目	+	+	—	—	—	—
埃笠姆鲱目	+	?	—	—	—	—
鲤形目	+	+	+	+	+	+
江汉鱼科	—	—	—	+	—	—
鲤科	+	+	+	—	+	+
鳅科	—	+	—	—	—	—
鲇形目	+	+	—	+	+	—
鲈超目	+	—	—	+	—	—
鲈形目	—	—	—	+	—	—
鰕虎鱼目	+	—	—	—	—	—

a) “+”, 有; “—”, 尚未发现

本区域古近纪鱼类以淡水鱼类为主,说明当时水域无疑为淡水环境,但茂名盆地可能为海水生活的鲨鱼化石及鲎化石、宁明盆地可能栖居于海水或咸水的鲱超目及鰕虎鱼目化石,提示该区域古近纪时有可能受过海水的影响.最近10多年,我们对上述一些鱼化石做了描述和初步研究,取得了一些初步的结论,具体如下.

2.1 鲤形目化石

2.1.1 江汉鱼科化石

王将克等人^[2]描述了一批三水盆地古新统埭心组—始新统华涌组的鱼化石,认为该鱼群包括鲤形目鲤科的4个亚科. Chang等人^[37,38]指出,三水的“鲤科”化石无论从描述还是图版上看,均不具有明显的鲤科特征. 其中,王将克等人^[2]将采自塍西和红岗采石场的一些标本归入鲤科骨唇鱼(纹唇鱼)属,订立新种三水纹唇鱼†*Osteochilus sanshuiensis*,并主要依据背鳍条较长将同样采自塍西的标本订为新种长鳍纹唇鱼†*Osteochilus longipinnatus*,主要依据体型较高将采自红岗的标本订立新种宽体纹唇鱼†*Osteochilus laticorpus*. 古脊椎所近年来在三水盆地野外发掘,于红岗采石场采到形态上与上述纹唇鱼相当接近的标本(图2). 根据新采集到的材料与已发表的描述、图版对比,本文第二作者新近研究认为,上述3种“纹唇鱼”具有明显的江汉鱼特征,如神经棘与体高比例显著小于同时期的鲤形目鱼类、尾柄高略大于尾柄长等,均应归入江汉鱼科. 再者,江汉鱼科鱼类具显著幼鱼体窄、成鱼体高的自体发育特征^[39],不宜将体高差异作为宽体纹唇鱼(体长79 mm,王将克等人^[2]: P.10)与三水纹唇鱼(体长68 mm,王将克等人^[2]: P.10)种间差异的鉴别特征;长鳍纹唇鱼背鳍中后部鳍条保存不完整导致前端鳍条显得比较突出,“长背鳍”不宜作为与三水纹唇鱼区分特征^[39]. 此外,长鳍纹唇

图2 三水江汉鱼
Figure 2 †*Jianghanichthys sanshuiensis*

鱼具显著江汉鱼幼鱼特征: 体形纤细、骨骼不够粗壮、尾柄较窄等; 原作者对该种的测量值也证实这一推测(测量体长39 mm, 王将克等人^[2]: P.10). 综合以上, 建议将上述纹唇鱼3种合并修订为三水江汉鱼†*Jianghanichthys sanshuiensis*一种, 种征在新材料的基础上补充、修订, 并进一步与湖北江汉鱼†*Jianghanichthys hubeiensis*及相邻层位的江汉鱼材料详细比较.

2.1.2 鲤科化石

鲤科是淡水鱼类中最大的科, 有约367属3006种^[3]. 多数学者赞成鲤科分为雅罗鱼系和鲴系^[44,45], 但亚科的划分迄今尚未取得较为一致的意见^[3,44~48]. 本文所用亚科主要依据中国学者, 如伍献文^[49,50]的划分.

本区的鲤科化石有鲤亚科(Cyprininae)、东亚特有类群(鲃亚科Cultrinae和鲴亚科Xenocyprinae及其相关鱼类)、鲃亚科(Barbinae)等多种. 鲤亚科现今分布于亚洲和欧洲, 以亚洲的种类较为丰富, 仅有鲤鱼*Cyprinus carpio*断续分布于东亚和欧洲, 以及黑鲫*Carassius carassius*分布于欧洲^[46,48]. 古近纪的鲤亚科化石目前仅见于本区域, 其中最早的是产自广东茂名盆地上始新统的茂名始原鲤(†*Eoprocyrpris maomingensis*)^[32]. 1957年, 刘宪亭^[1]研究了一尾产自茂名盆地油柑窝组钻井岩芯中的鲤科化石, 将它归入鲤亚科鲤属(*Cyprinus*), 定名为“茂名鲤(†*Cyprinus maomingensis*)”, 并据此认为含鱼化石层的时代为中新生世. 实际上, 该标本保存欠佳, 除了末根不分枝背、臀鳍条均为具锯齿的硬棘这一鲤亚科特有的性状外, 并无其他可归入鲤属的可靠特征^[38]. 近年, 古脊椎所等在同一化石点采到了至少3个属种的鲤科化石. 根据原有标本, 结合新采集到的标本, 我们对其中的“茂名鲤”做了重新研究. 结果显示, 其咽齿呈匙形(图3(a)); 明显不同于鲤属的臼齿型咽齿, 而与原鲤属(*Procyrpris*)的较为相似, 但它的背鳍分支鳍条数目和脊椎骨数目明显少于原鲤属的, 因此我们将“茂名鲤”修订为茂名始原鲤^[32]. 产自印尼苏门达腊中部始新世的始鲤属†*Eocyprinus*, 曾被认为属于鲤亚科^[52], 但其臀鳍末根不分枝鳍条后缘不带锯齿、分支鳍条有7根, 显然不可能属于末根不分枝臀鳍条后缘带锯齿、不分枝臀鳍条一般仅有5根的鲤亚科^[13]. Danil'chenko^[53]曾指出古近纪有鲤属化石, 但没有给出化石的描述及图版.

图3 古近纪鲤亚科咽齿比较。(a) 茂名始原鲤；(b) 粗棘花山鲤；(c)，(d) 伍氏南宁鲤。A, B, C, 分别表示最内侧行(主行)齿、外侧行齿和最外侧行齿。编号1, 2, 3, 4, 分别表示第1~4枚咽齿。L, r, 分别表示左、右侧。依据文献[13,32,51]

Figure 3 Morphology of cyprinid pharyngeal teeth during Palaeogene. (a) *†Eoprocypis maomingensis*, (Chen et al), 2015; (b) *†Huashancyprius robustispina*; (c), (d) *†Nanningocyprius wui*. Abbreviations: A, B, and C standing for main row, outer row, and outmost row of pharyngeal teeth, respectively. Tooth position is numbered from anterior to posterior in each row^[13,32,51]

鲤亚科鱼类在渐新世有了明显分化,如在宁明盆地出现了粗棘花山鲤 $\dagger$ *Huashancyprius robustispina*^[13],在南宁盆地则有伍氏南宁鲤 $\dagger$ *Nanningocyprius wui*^[53]。这两个属的咽齿(图3(b)~(d))均呈臼齿型,且咀嚼面上都有一条沟纹(主行第一枚除外),与鲤属尤其是属中较原始的抚仙鲤(*Cyprinus fuxianensis*)和小鲤(*C. micristius*)较相似。但粗棘花山鲤以背、臀鳍末根不分枝鳍条特别粗壮,咽齿主行第二、第三枚齿侧面有许多皱褶区别于其他属种;伍氏南宁鲤以齿式3-2-1(即第二行咽齿数比鲤属和花山鲤属的多一枚),主行第一枚咽齿明显较大,咽齿咀嚼面仅有一条沟纹为主要特征。

发现于宁明盆地渐新统宁明组的宁明生态鱼 $\dagger$ *Ecocarpia ningmingensis*^[12](图4),鱼体细长而侧扁,臀鳍基较长,腹鳍骨分叉浅等特征与鲃亚科的相似;但其咽齿侧扁,主行齿有6或7枚,明显不同于鲃亚科而与鲴亚科的相似;其背鳍第一根不分枝鳍条短,且与第二根不分枝鳍条相接触,显然与鲃亚科和鲴亚科的都不同。为确定生态鲤的系统位置,借用Cavender和Coburn^[45]的矩阵,在矩阵中加入生态鲤及其相应的特征编码,然后用PAUP4.0b 10软件,用分枝界限(branch and bound)搜索方法,得到一棵最短的、拓扑学特征与Cavender和Coburn^[45]的系统树非常相似的分支树,结果显示,宁明生态鱼与鲃亚科+鲴亚科构成姐妹群^[12]。鲃亚科和鲴亚科是鲤科中分布局限于东亚的两个类群,产生于东亚特殊的自然环境中^[47]。近年,德国和越南学者在越南北部纳堂盆地及高平盆地采到了鲃亚科和鲴亚科的化石,虽然仅有零散的咽齿^[4,5]。该含鱼化石层的时代,原根据孢粉研究认为是渐新世,后根据哺乳动物,尤其是石炭兽化石研究认为是晚始新世早-中期^[54]。

2.1.3 鳅科化石

现生鳅科鱼类广泛分布于亚洲、欧洲及非洲西北部。与丰富的现生鱼类相比,已发现的鳅科化石极其稀少,尤其是古近纪的鳅科化石。目前已知的化石地点仅有两个:一个是南宁盆地邕宁组,另一个是德国巴伐利亚北部上渐新统。南宁的鳅科化石均为眼下刺,没有完整的鱼体^[24],德国的也是如此^[55]。南宁鳅($\dagger$ *Cobitis nanningensis*)(图5)的眼下刺长1.8~3.0 mm,粗细适中,刺二分叉,侧后突较中后突短而细,长度约为中后突长的1/3,侧突发育,与德国的 $\dagger$ *Cobitis primigenus*^[55]较为相似,但又以侧突更为发育而与

图4 宁明生态鱼†*Ecocarpia ningmingensis*. (a) 正型标本 NMV 41702; (b) 放大的正型标本的头部; (c) 咽齿NMV 41503a, 腹面视; (d) 咽齿NMV41503b, 咀嚼面视. art, 关节骨; br.b, 鳃条骨; d, 齿骨; dpt, 膜质翼耳骨; fr, 额骨; ioc, 下眶感觉管; iop, 间鳃骨; la, 泪骨; le, 侧筛骨; mc, 下颌感觉管; mx, 上颌骨; kie, 动筛骨; op, 鳃盖骨; pa, 顶骨; pl, 腭骨; pmx, 前上颌骨; pop, 前鳃骨; pte, 后颞骨; sb, 鳞片骨; scler, 巩膜环; so, 上眶骨; sop, 下鳃骨. 依据Chen等人^[12]

Figure 4 †*Ecocarpia ningmingensis*. (a) Holotype; (b) head of the holotype; (c) pharyngeal teeth in ventral view; (d) pharyngeal tooth in grinding surface view. Abbreviations: art, article; br.b, branchiostegal rays; d, dentary; dpt, dermopterotic; fr, frontal; ioc, infraorbital sensory canal; iop, interopercle; la, lacrimal; le, lateral ethmoid; mc, mandibular canal; mx, maxilla; kie, kinethmoid; op, opercle; pa, parietal; pl, palatine; pmx, premaxilla; pop, preopercle; pte, posttemporal; sb, scale bone; sclera, sclerotic; so, supraorbital; sop, subopercle. After Chen et al.^[12]

之区别^[24].

综上所述, 本区古近纪鲤形目化石有江汉鱼科、鲤科和鳅科. 世界范围内, 迄今已报道的鲤形目化石有: 鲤科、亚口鱼科(Catostomidae)、鳅科、条鳅科(Nemacheilidae)和江汉鱼科^[38,39,56]. 其中, 条鳅科化石出现较晚, 吉尔吉斯斯坦中-晚中新世的条鳅化石是该科迄今最早的化石记录^[56]; 其他4个科在古近纪均已化石出现, 具体如下: (1) 迄今最早期(始新

世)的鲤科化石仅见于亚洲东部和中部及东南部, 如中原油田(河南范县)^[57]、河南南阳盆地^[58]、渤海沿岸^[59]、新疆准噶尔盆地^[60]、广东茂名盆地^[1,32]、广西百色盆地^[26]、越南北部纳塘盆地和高平盆地^[4]、哈萨克斯坦东部斋桑盆地^[61]、印尼苏门达腊中部^[51]. 一些学者^[61,62]认为斋桑盆地早-中始新世的†*Parabarbus*是世界上最早的鲤科化石记录, 尽管保存的仅为数十枚下-中始新统及下渐新统的咽齿, 而原作者给出的

图5 南宁鳅†*Cobitis nanningensis*. (a) 正型标本NHMG 011653.1, 侧视; (b) 正型标本NHMG011653.1, 背视; (c) NHMG 011653.2, 腹侧视; (d) NHMG 011653.2, 背侧视。Lcp, 侧后突; lp, 侧突; lrp, 侧吻突; mcp, 中后突; mp, 中突; mrp, 中吻突。标尺长度为0.5 mm。依据Chen等人^[24]

Figure 5 †*Cobitis nanningensis*. (a) Holotype NHMG 011653.1, lateral view; (b) holotype NHMG 011653.1, dorsal view; (c) NHMG 011653, lateroventral view; (d) NHMG 011653, laterodorsal view. Abbreviations: lcp, laterocaudal process; lp, lateral process; lrp, laterorostral process; mcp, Mediocaudal process; mp, medial process; mrp, mediorostral process. Scale bars equal to 0.5 mm. After Chen et al.^[24]

插图和图版是一枚下渐新统咽齿,对咽齿的描述和比较中只提到咀嚼面和齿冠形状和*Parabarb*相似。欧洲最早的鲤科化石是见于捷克波西米亚地区渐新世早期的鲃亚科鱼类^[63],这也是欧洲目前唯一的早渐新世化石;欧洲中-晚渐新世除鲃亚科外还有雅罗鱼亚科^[64];北美最早的鲤科化石见于渐新世中-晚期^[64],均为雅罗鱼亚科;非洲最早的鲤科化石见于中新世^[65]。其他地区未有鲤科化石的报道,也没有现生鲤科的分布。(2) 亚口鱼科最早的化石是发现于北美古新世的零散骨片^[66],始新世亚口鱼科呈跨太平洋分布于东亚和北美,渐新世时亚口鱼科在亚洲仍见于哈萨克斯坦东部、俄罗斯远东地区和蒙古,但在北美仍分布很广^[38,67-70]。(3) 目前鳅科古近纪的化石极其稀少,仅在南宁盆地渐新世早-中期和德国渐新世晚期有所发现^[24,55]。但这些化石的发现说明,渐新世时鳅科已广泛分布于欧亚大陆。(4) 江汉鱼科是新近根据湖北松滋始新世洋溪组的湖北江汉鱼的重新描述而建立起来的化石科^[71]。湖北江汉鱼最早被归入鲤科^[72],后来被认为有可能属于亚口鱼科^[38]。江汉鱼科目前仅见于我国湖北松滋、湖南临澧和广东三水的古新世-始新世地层^[39]。可见,环北部湾地区是世界上迄今发现了早期(古近纪)鲤形目科一级类群最多的区

域,其中江汉鱼科的三水江汉鱼†*Jianghanichthys sanshuiensis*、鲤科的茂名始原鲤†*Eoprocyrpris maomingensis*、和鳅科的南宁鳅†*Cobitis nanningensis*分别是各科最早期的化石记录,代表着鲤形目主要分支的分异时间和早期形态。此外,本区古近纪鲤科化石以鲃亚科、鲃亚科和鲃亚科等东亚特有类群以及鲃亚科为主,不同于较北或较高纬度地区基本上以雅罗鱼亚科和鲃亚科为主^[57-60,63,64],也不同于中亚和我国青藏高原地区以鲃亚科(包括裂腹鱼亚科)为主^[38,61,73-75],而与越南北部的较为相似。而且,东亚特有类群的出现通常认为是与东亚特有的气候相关。

2.2 鲃超目化石

鲃超目化石在本区主要发现于宁明盆地渐新统宁明组,在南宁盆地渐新世邕宁组也有发现。宁明的鱼化石体型较大,长达500多毫米,臀鳍基长,背棱鳞数目多,背棱鳞表面有纹饰,前角舌骨中央具一大孔,第一末端尾椎不明显变小,第一尾神经骨向前延伸不与第一尾前椎愈合形成尾杆骨等特征显示,宁明的鲃超目化石明显不同于鲃形目而隶属于埃笠姆鲃目^[14]。由于其镶嵌组合的形态特征,目前还难以把它归入已知的科、属,需要提取形态特征做系统发

育分析. 南宁的鲱超目标本可能也属于埃笠姆鲱目. 埃笠姆鲱目是鲱超目中呈世界性分布且已灭绝的鱼类类群, 其化石曾发现于我国浙江东部下白垩统^[76,77]和渤海沿岸始新统中部^[59,78], 以及南美、北美、非洲和欧洲早白垩世-中始新世的海相和非海相地层中^[79,80]. 这些化石在广西渐新统的发现, 扩大了埃笠姆鲱目的地史和地理分布范围.

2.3 鰕虎鱼目化石

鰕虎鱼目化石迄今报道的不多, 我国则尚未有过报道. 迄今最早的鰕虎鱼目化石出现于意大利^[81]和印度西部^[82]的下始新统, 但后者仅有耳石化石. 中始新世至晚渐新世, 鰕虎鱼目化石地点虽然略有增加, 但一些地点仅有耳石化石^[82,83], 鱼体骨骼化石仅见于欧洲几个地点: 如, 英国怀特岛晚始新统^[84]、法国上莱茵省、意大利和德国东部早渐新统^[84,85]、法国南部晚渐新统^[85]及捷克渐新统^[86,87]. 西班牙东北部中始新统也有鱼体化石发现, 但化石保存不好^[88]. 我们在宁明盆地发现的鰕虎鱼目2个种的鱼体化石可以说是古近纪该类化石在欧洲以外区域的首次发现.

2.4 鲈形目化石

鲈形目鱼类最早出现于欧洲(法国、瑞典)白垩纪最晚期的海相地层中, 至始新世遍布世界海水及淡水水域. 在我国东部及南部始新统非海相沉积中也常有鲈形目鱼类发现, 主要是系统位置尚不明确的低等鲈形目鱼类洞庭鳊属*Tungtingichthys*^[89-91]. 三水发现的鲈形目化石也被王将克等人^[2]归入洞庭鳊属.

2.5 鲇形目化石

世界上最早的鲇形目鱼类发现于上白垩统, 如南美上白垩统的海鲇科Ariidae化石、阿根廷和玻利维亚上白垩统的重颌鲇科Diplomystidae化石. 古近纪鲇形目几乎遍布世界各地^[3]. 我国已记述的古近纪鲇化石仅有鲇科的2属3种, 分别产自湖南湘乡^[90]和广东三水^[2], 及渤海沿岸数枚鲇科的胸鳍刺和背鳍刺^[59]、南宁盆地半截鲇科的胸鳍刺^[92]. 新近在茂名盆地发现的鲇化石保存较好且可能属于生活于海水的类群. 在南宁盆地新发现的鲇化石不仅有数量较多的鳍刺, 还有头部骨片. 这些化石的研究不仅可为了了解鲇形目鱼类的早期形态、分布、分化和演化提供重要依据, 或许也可以为判断当时这一地区是否发生

过海侵提供依据.

2.6 骨舌鱼目化石

骨舌鱼目鱼类主要生活于淡水, 仅有个别可进入咸水^[3]. 人们较熟悉的金龙鱼*Scleropages*即属于骨舌鱼类. 金龙鱼属化石曾发现于印度白垩纪末期、非洲白垩纪末期或古近世晚期、欧洲古近世、苏门答腊始新世和澳大利亚渐新世, 及我国湖南湘乡下始新统下湾铺组和湖北松滋下始新统洋溪组^[93]. 骨舌鱼科的化石还见于古近纪的北美、欧洲和非洲^[3]. 三水骨舌类化石的研究对于更全面的诠释骨舌鱼类的跨洋分布及了解当时的古地理格局都将提供重要证据.

2.7 鲨鱼类化石

鲨鱼类是世界性广泛分布的鱼类, 其化石最早出现于二叠纪末或三叠纪初, 侏罗纪-白垩纪时已广泛分布于世界各地^[3]. 古近纪的鲨鱼化石也很丰富^[3], 但就笔者所知, 我国目前还没有报道过. 鲨鱼化石具有重要的指相意义, 而且, 就目前所知, 许多鲨鱼类现生科最早的化石出现于古近纪, 如豹纹鲨科*Stegostomatidae*, 鲸鲨科*Rhincodontidae*, 长尾鲨科*Alopiidae*和半沙条鲨科*Hemigaleidae*等^[3]. 因此, 茂名鲨鱼化石的研究对于了解鲨鱼类的演化和判断当时是否发生过海侵都有重要意义.

3 研究展望

综上所述, 本区古近纪鱼化石数量和种类丰富, 为追溯现代鱼类区系的起源演化提供了重要证据. 其中的鲤形目化石出现的时代早, 多样性高, 在鲤形目起源和早期演化研究中具有重要的、不可替代的作用. 此外, 本区域始新世与渐新世鱼群中鲤形目目下类群组成有明显不同, 与东亚其他区域相似, 始新世江汉鱼科或亚口鱼科相当繁盛, 晚始新世之后鲤科鱼类代之而起. 鱼群这一演替过程的机制和环境背景研究, 或许对于我们更全面地了解始新世/渐新世全球性气候变化事件具有重要意义.

另外, 本区鱼群中首次发现于渐新世地层的埃笠姆鲱目化石, 为了解该类群的演化和迁徙提供了新的资料. 而且迄今没有在远离海岸的内陆盆地发现过该类化石, 而现生鲱超目鱼类一般生活于海水中, 很多种类为迴游鱼类, 能溯河而上. 首次发现于中国的鰕虎鱼目化石, 其现生种类主要生活于海水

和咸水,偶尔出现于淡水.本区常见的鲃形目鱼化石,其现生种类或栖居于淡水或生活于海水;鲨鱼类基本生活于海水.因此,本区这些鱼化石的研究对于探讨当时的古地理、古环境亦有指示意义.

总之,环北部湾陆上盆地古近系鱼化石为重建该区域古近纪鱼类区系、有关类群的起源演化及其古地理分布格局、当时是否发生过海侵等提供了实证.

然而目前已研究的化石不多,许多化石材料有待于详细的形态学和系统学研究.加大力度进一步的采集研究标本也很有必要.在未来研究中,更细致的地层工作、应用新的技术手段(如高精度CT扫描、硬X线荧光扫描)和分析方法(如各种系统发育分析软件的应用)、多学科的结合(如结合分子生物学)将会取得更好的成果.

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Summary for “新生代早期鱼类演化的热点区域：环北部湾陆上盆地古近纪鱼化石研究成果与展望”

Evolutionary hotspot of Cenozoic fish: Paleogene ichthyofauna from the onshore basins around Beibu Gulf

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Paleogene sediments are well developed in the onshore basins, including Ningming, Nanning, and Baise Basins of Guangxi, Sanshui and Maoming Basins of Guangdong, and Changchang Basin of Hainan, around the Beibu Gulf (Gulf of Tonkin). A large number of fish fossils have been recovered from these sediments. As our fieldwork and research activities progressed in recent years, the picture of the Paleogene ichthyofauna is gradually unveiled. Here we review the systematic paleontology of the fossil fishes and their implications on paleoecology and paleobiogeography. Known Paleogene fossil fishes from this region include cypriniforms, osteoglossiforms, siluriforms, and perciforms from Sanshui Basin; cypriniforms, siluriforms and sharks from Maoming Basin; cypriniforms from Changchang Basin; cypriniforms, siluriforms, and clupeomorphs from Nanning Basin; cypriniforms, †ellimmichthyiforms, siluriforms, and gobiiforms from Ningming Basin; and cypriniforms from Baise Basin.

Among all these fossil fishes, cypriniforms, a group of primary freshwater fishes, were the dominant fishes in terms of specimen numbers and taxonomic diversity, which spanned from the Paleocene to the Oligocene and occurred in every basin of this region. Described cypriniforms from this region include (1) Cyprinidae: †*Eoprocyrpris maomingensis* from late Eocene Youganwo Formation of Maoming Basin; †*Huashancyrpris robustispina* and †*Ecoparpia ningmingensis* from Oligocene Ningming Formation of Ningming Basin, and †*Nanningocyrpris wui* from Oligocene Yongning Formation of Nanning Basin; (2) Jianghanichthyidae (the only fossil family of the order Cypriniformes and only occurred in South China): †*Jianghanichthys sanshuiensis* from Paleocene Buxin Formation of Sanshui Basin; and (3) Cobitidae: †*Cobitis nanningensis* from Oligocene Yongning Formation of Nanning Basin. These fishes are among the oldest cypriniform fossils, which provide critical information on the origin and evolution of the largest extant freshwater fish order Cypriniformes. Moreover, Oligocene †ellimmichthyiforms (Clupeomorpha) and gobiiforms (Percomorpha) are important discoveries from this region. The former represents the first discovery of †ellimmichthyiform from the Oligocene worldwide which is younger than its known fossil records. The latter is the first occurrence of fossil gobiiforms in China. Furthermore, the most abundant Paleogene fishes of this region are cypriniforms, which are strict freshwater fish. Meanwhile, shark materials are also discovered along with possibly marine †ellimmichthyiform and siluriforms. The combination of above fishes indicates that the freshwater bodies of this region were invaded occasionally by marine water during the Paleogene.

To conclude, the Paleogene ichthyofauna from onshore basins of Beibu Gulf consists of oldest fossils of major clades of Cenozoic fishes and a relict of typical Mesozoic fish taxa, which suggest that this region is an evolutionary hotspot of Cenozoic freshwater fishes, especially of cypriniforms. The vertebrate paleontology, systematics, taxonomy, and paleoecology of the fish assemblages from this region are pending further study. To understand the origin and divergence of the major clades of the Paleogene fish, as well as hypothesize on the development of the recent fish fauna of East and South Asia, we suggest conducting more comprehensive fieldwork to collect scientifically valuable specimens in the onshore basins around Beibu Gulf, and performing in-depth laboratory research using traditional paleontological methods, 2-D and 3D computational tools, and molecular data of related extant fishes.

onshore basins around Beibu Gulf, Palaeogene ichthyofauna, evolution, palaeoenvironment

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