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湖南省境内洞庭鳜(*Tungtingichthys*, 鲈形目 Perciformes)的重新观察[1)]

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摘要 对秀丽洞庭鳜作了较详细的描述,在骨骼学特征和变异范围方面作了较多的补充。指出秀丽洞庭鳜和下湾铺洞庭鳜在背鳍前骨式、栉的形状和尾鳍前短鳍条数目等特征存在差异。补充了洞庭鳜的属征,并认为始新世化石低等鲈形目鱼类中北半球的洞庭鳜、*Amphiperca*、*Priscacara* 之间的关系比它们和南半球的 *Percichthys* 的关系更接近。

关键词 湖南,始新世,洞庭鳜,重新描述,比较

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1 前 言

化石鲈形目鱼类,特别是低等鲈形目鱼类的分类,至今仍是一个十分棘手的难题。一方面是由于现生鲈形目鱼类种类繁多(约 9293 种,据 Nelson, 1994),到目前为止,对现生鲈形目鱼类的系统发育尚缺乏全面的认识,化石鲈形目鱼类的系统分类研究便缺少了可靠的参证系统;另一方面,由于保存和修理工作方面的原因,化石低等鲈形目鱼类的形态学研究还不够深入,使研究者对于这类分化程度较低的鱼类的祖征、离征的区别以及对它们的分析无从下手。

鲈形目鱼类最早出现在欧洲(法国、瑞典)白垩纪最晚期海相沉积中(Patterson, 1964),到了始新世已成为世界海水及淡水水域中广布的鱼类。中国也不例外,洞庭鳜便是始新世广布于中国东部及南部淡水沉积中的一种低等鲈形目鱼类。对于中国这一类化石的进一步研究不仅能增添我们对低等鲈形目鱼类的骨骼形态学的认识,从而充实分类学研究的根据,而且通过对各大陆低等鲈形目鱼类间关系的研究也能为它们生存时代的动物地理格局提供重要的信息。

刘东生等(1962)首先描述了发现于湖南临澧歇架山孙家桥、石门三板桥始新世歇架山系孙家桥层的秀丽洞庭鳜(*T. gracilis*),建立了洞庭鳜属。此后,又不断发现了许多产洞庭鳜的地点和新的材料,其中有些被订为新种,如发现于湖南湘乡下湾铺下湾铺组的下湾铺

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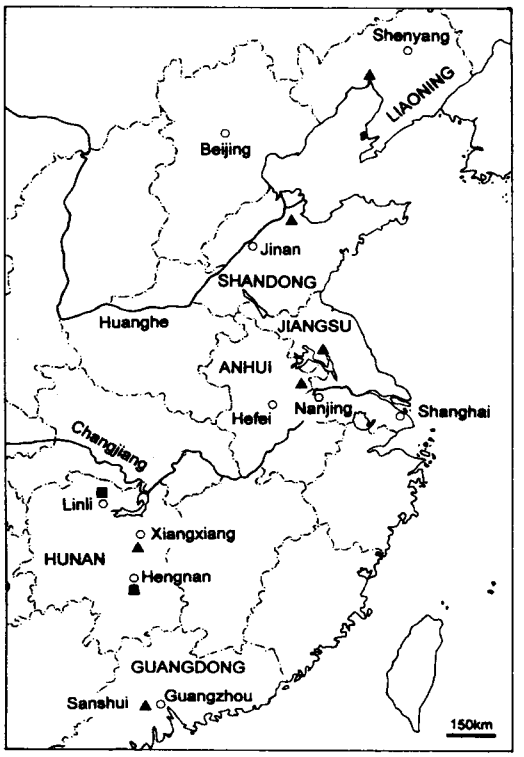

图 1 洞庭鳜的分布 ○为地名，■为正型标本产地，▲为其他标本产地

Fig.1 Sketch map of distribution of *Tungtingichthys* ○cities, ■locality of type species, ▲other localities

洞庭鳜(*T. hsiawanpuensis*，郑家坚，1962)，安徽来安张山集舜山集组的来安洞庭鳜(*T. laianensis*)，江苏洪泽阜宁组四段的洪泽洞庭鳜(*T. hongzeensis*)(夏树芳等，1979)，广东三水盆地垅心组的秀丽洞庭鳜(王将克等，1981)，湖南衡南金甲乡龙湾滩采石场茶山坳组的秀丽洞庭鳜(见下文)，以及山东博兴、辽宁盘山沙河街组三段下部—四段上部(钻井中)的始新洞庭鳜(*T. eocaenus*)(张弥曼等，1985)(图 1)。

由于绝大多数地点的化石都产自油页岩，修理工作十分困难，无法详细观察骨骼形态特征。经试用酸处理法、喷砂法等多种修理方法均收效甚微，只能仍采用机械方法，个别标本采用了近来国外普遍运用的"转移法"(transfer method)，即在标本的一面修理完毕后，将此面包埋在透明的玻璃胶中，翻过来再修理另外一面，使标本的两面都能显示。通过对新近修理的标本的观察，我们得到了比过去更多的形态学方面的信息。本文即在此基础上对秀丽洞庭鳜作一较详细的描述，对洞庭鳜属的特征作出补充，并对低等鲈形目鱼类的系统关系进行一些粗浅的讨论。同时，也借此机会将目前鲈形目鱼类系统研究的困难情况介绍给读者。

本文研究材料包括中国科学院古脊椎动物与古人类研究所收藏的产于湖南的洞庭鳜标本，计有刘东生等研究过的标本 V1043，V1043.1–3；郑家坚所研究的标本 V1105，V1105.1–3；张弥曼等研究的标本 V5603 以及新近采自湖南临澧石门三板桥的标本 V11367.1–44以及湖南省地质局区测队第六分队蔡和气采自三板桥并送交古脊椎所鉴定的标本 V11368.1–12。同时我们还选取了现生鲈形目鱼类翘咀鳜(*Siniperca chuatsi*)和鲈鱼(*Lateolabrax japonicus*)作为对比标本。

2 标本记述

鲈超目 Percomorpha Rosen, 1973

鲈形目 Perciformes Regan, 1913

亚目及科未定 Suborder and Family indet.

洞庭鳜属 *Tungtingichthys* Liu *et al.* 1962

修订属征 体型较低的小鱼，已知最大体长约 63mm，体高为体长的 27%—38%。侧

扁。上枕脊上缘加厚，有上枕骨骨架。眶径大于眶前距。口端位或亚上位。上、下颌口缘具绒毛状齿。前上颌骨前端具上升突及关节突。有细小的辅上颌骨。腭骨具细齿。鳃盖骨后缘有一棘，前鳃盖骨后缘及下缘具锯齿，后缘齿较密集，下缘齿较稀疏、宽大。鳃条骨6根。泪骨下缘具较大的锯齿。上、下咽骨具臼状咽齿。背鳍鳍棘部分和鳍条部分连续，鳍棘部分基部长于鳍条部分，两部分间有一浅凹刻，鳍棘Ⅷ–X根，最后一根鳍棘稍长于倒数第二根鳍棘，鳍条8—11根。背鳍前骨(predorsal)3根，背鳍前骨式在秀丽洞庭鳜中为0/0/0 + 1/，第一支鳍骨支持一鳍棘；在下湾铺洞庭鳜中为0/0/0 + 2/，第一支鳍骨支持二鳍棘。臀鳍具有Ⅲ鳍棘、7—9鳍条，第二鳍棘最粗壮，第一支鳍骨载有两根鳍棘。胸鳍条约13—15根。腹鳍胸位，具Ⅰ鳍棘，5鳍条。尾鳍浅分叉或截形。尾骨骼为低等鲈形目鱼类中所常见的类型，第一尾前椎(preural centrum 1)与第一末端尾椎(ural centrum 1)愈合，无独立的第二末端尾椎。尾下骨5枚。尾神经骨2枚，第一枚前腹端扩大成尾盖骨。尾上骨3枚。第二尾前椎上的神经棘在大部分标本中短，但在少数标本中也有长的神经棘。椎骨24—25枚。体被栉鳞(ctenoid)，颅顶后部及颊部由圆鳞(cycloid)或栉鳞覆盖。

秀丽洞庭鳜 *Tungtingichthys gracilis* Liu, Liu et Tang, 1962

产地、层位及时代　湖南省临澧县歇架山孙家桥，石门三板桥，歇架山组；始新世。

修订种征　背鳍前骨式0/0/0 + 1/，背鳍棘在多数个体中为Ⅷ根，少数个体中为Ⅸ根，臀

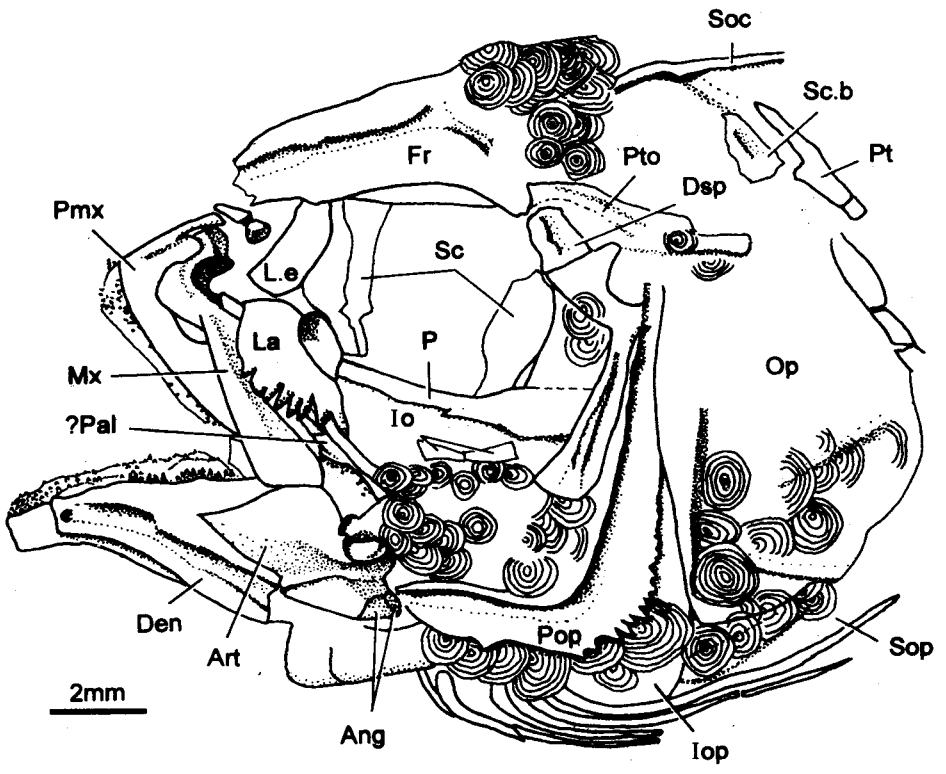

图2　秀丽洞庭鳜头骨左侧视

Fig.2　*T. gracilis*, skull in left view, V11367

鳍条 7—8 根。鳞片上的栉短而钝。尾鳍上、下主鳍条外侧各有短鳍条 12 根。

标本描述 鱼体小、较低，体长约 31—63mm。侧扁。最大体高位于腹鳍起点处，体长约为体高的 2.6—3.3 倍，头长的 2.5—2.9 倍(图 2；图版 I)。以下描述主要根据新近采自三板桥的 V11367 以及正型标本 V1043，并参考其他标本。

头骨：头中等大，头长略大于头高(图 2)。

脑颅：颅顶的长形额骨表面光滑，前部稍窄，自眼眶中部之后逐渐增宽，自其前端至后外侧有眶上感觉管穿过；顶骨小，形状不规则。上枕骨前端分开二顶骨插入二额骨后部，有向后突出的、略为高耸的上枕脊，脊的上缘加厚，有上枕骨骨架。二额骨前方有中筛骨略插入其间，中筛骨前部有两个模糊的小突起，与前上颌骨的上升突关节。鼻骨位于中筛骨的两侧，长条形，上有感觉管开口。中筛骨两侧还有较厚的侧筛骨，由于挤压而变形，其上边缘与额骨相接，后缘构成眼眶的一部分，下部为泪骨所覆盖。眼眶较大，眶径大于眶前距。眼眶内可见巩膜环(sclerotic ring)，似由两个薄片组成。副蝶骨较粗壮，贯穿眼眶下部，前端位于侧筛骨内侧，向后在眼窝后缘有伸向背侧方的上升突(ascending process)。在上升突的前方可以看到弯曲的基蝶骨(basisphenoid)的前支。眼窝的后上部内侧可见片状的翼蝶骨(alisphenoid)。在脑颅中部、翼蝶骨外侧，可以看到蝶耳骨(sphenotic)与舌颌骨相关节的关节窝处的骨骼加厚部分，蝶耳骨上缘前部接额骨，后部接翼耳骨(pterotic)。翼耳骨略长，因挤压而破碎，腹侧部与蝶耳骨的腹侧部一同构成与舌颌骨关节的关节窝；外表面有自额骨延伸过来的感觉管，向后进入后颞骨(posttemporal)腹支。上耳骨(epiotic)由于挤压而破碎，仅保存了两个明显的小突起，与后颞骨的背支相连接。后颞骨向前伸出两支，背支长而尖，附于上耳骨，腹支短而圆，支撑于翼耳骨上，骨片表面有自翼耳骨经鳞片骨(scale bone)延伸过来的感觉管。后颞骨背、腹支间有三角形薄片状的鳞片骨，其上有交叉的感觉管，向颅顶中部延伸的一支接横枕管，水平的一支前接翼耳骨上的感觉管，后接后颞骨上的感觉管。

颌部：口裂中等大小，下颌与方骨关节处略前于眼眶中点。口缘由前上颌骨和齿骨组成。前上颌骨前端有一向上的细长上升突，上端尖。其侧方为略宽短的关节突，上端圆。前上颌骨口缘有绒毛状齿组成的齿带。上颌骨位于前上颌骨后方，长形，后部宽而扁平，前部变窄，前端为分叉的关节突，与前上颌骨相关节。其后为腭骨的前方突起。在 V11367.14 标本上颌骨后上方可见一小的细长条形辅上颌骨，在其他标本上尚未观察到。齿骨略呈三角形，口缘有绒毛状齿，后端分叉，为关节骨插入处。关节骨前端尖，插入齿骨后叉中，背缘隆起，为上颌骨所遮盖，后背方有和方骨(quadrate)关节的关节窝，后腹端有两块小的隅骨(angular)。

腭部：腭骨(palatine)大部被泪骨(lachrymal)及其他骨片所覆盖，仅见其前方的棒状突起及后方与外翼骨(ectopterygoid)相接的细长突起，V11367 标本中上颌骨之后外翼骨之前腭骨下方有许多细齿，估计应为腭骨腹面的齿。内翼骨(entopterygoid)为长半圆形薄片状。外翼骨为约呈直角的弓形，背缘接内翼骨，后缘接方骨。内、外翼骨内面均无齿。方骨呈三角形，下缘加厚，前下方有关节突和关节骨的关节窝相关节，细长的续骨(symplectic)自方骨后缘下方插入。方骨后上方、内翼骨后下方为薄片状的后翼骨，形状不清。

颊部：围眶骨系列中保存较好的是泪骨，其腹缘有较大的锯齿，锯齿数目在不同的标

本上不一(约 5—9 个)，郑家坚(1962)和张弥曼等(1985)曾将此骨误认为腭骨，在新近修理的几块采自三板桥的标本上可以清楚看到这一骨片覆盖在副蝶骨之上(图 2，图版 I)，因此确为泪骨而非腭骨。泪骨后腹方、沿眼眶下缘有狭长的眶下骨，由于这些骨片下部均被鳞片覆盖，看不清它们的数目及形状。所见眶下骨眶缘略增厚，应为感觉管通过处。无眶上骨。鳃盖骨近三角形，前缘加厚，前下角尖，腹缘斜向后上方，由于后缘恰位于匙骨和上匙骨之上，在化石中通常被上述两个骨片挤碎，在大多数标本中都没能看到完整的后缘，加上颊部均被鳞片覆盖，很难看清鳃盖后缘是否有棘，但在至少两个标本(V11367.10 及 V11368.1)中，在腹缘和后缘的交会处修理出了一个清楚的棘(图 3)。此棘下方鳃盖骨下缘光滑，肯定没有其他棘突，棘的上方鳃盖骨后缘未见其他棘突，但是否确无棘突则无法完全肯定。鳃盖骨的前上方有一大的与舌颌骨连接的关节窝。前鳃盖骨上、下支相交成直角，上支较下支长，后缘及下缘均有锯齿，后缘锯齿较小，排列紧密，在有些标本中可多达 20 个左右，下缘锯齿排列不甚规则，后部约有 2—5 个排列较紧密的小齿，前部则为少量较宽大的齿或仅呈缺刻状。下鳃盖骨为前宽后窄的长条形骨片，前上方有一细长突起，插入鳃盖骨和间鳃盖骨之间。间鳃盖骨亦略呈三角形，在三板桥的标本中前、后下角均为圆弧形。

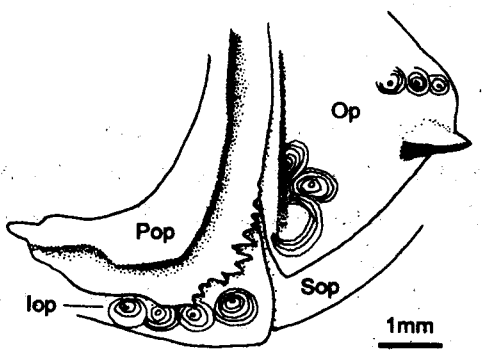

图 3　秀丽洞庭鳜鳃盖系统，示鳃盖后缘一棘
Fig.3　*T. gracilis*, opercular system, showing the spine at posterior margin of opercular, V11367.10

舌弓、鳃弓及鳃条骨：舌弓骨骼中舌颌骨保存较好，上部为扇形，下部为棒状。扇形扩展部分的基部有供颜面神经舌颌支(r. hyomandibularis V)通过的孔。另外，在头部下边缘可见部分角舌骨(ceratohyal)，尾舌骨(urohyal)的下缘以及前端棒状的基舌骨(basihyal)。鳃弓骨骼十分破碎，无法辨认角鳃骨(ceratobranchials)及咽鳃骨(pharyngobranchials)，也不知第五对角鳃骨是否愈合，仅就咽齿的分布情况来看，似乎上、下咽骨(upper and lower pharyngeals，即咽鳃骨及第五对角鳃骨)都有臼状齿(molariform-like teeth)。鳃条骨(branchiostegals)6 根。

肩带与鳍：上匙骨(supracleithrum)为狭长的骨片，前端狭窄，和后颞骨内侧连接，后端略扁平。匙骨(cleithrum)长大、弯曲，上端尖，拐角处向后伸展出宽平骨片，腹支长，宽大，略向前延伸。后匙骨 1(postcleithrum 1)被匙骨拐角处的宽平骨片所覆盖，仅能看到细棒状的后匙骨 2。肩胛骨(scapula)略呈四边形，中间有一圆孔，乌喙骨(coracoid)略似斧形。胸鳍位高，略呈扇形，鳍条约 13—15 根，少于 15 根的或许和保存情况有关。胸鳍基部有 4 个短棒状的胸鳍基骨(radials)，在 V11367.14 中似乎都只与肩胛骨而不与乌喙骨相关节，在 V11367 中情况略有不同，第三胸鳍基骨同时与肩胛骨和乌喙骨连接，而第四胸鳍基骨则与乌喙骨连接。腹鳍胸位，起点与背鳍起点相对或略后于背鳍起点，基鳍骨长大，不愈合，直接连于匙骨上，腹鳍具 I 粗壮鳍棘及 5 鳍条。

背鳍长，棘鳍部分和软鳍部分连续，棘鳍基部长于软鳍基部。背鳍式为Ⅷ-Ⅸ，8—

10，第一根鳍棘最短，第三、四根最长，其后鳍棘长度依次递减，最末一根鳍棘稍长于倒数第二根鳍棘，但比第一软鳍条稍短，因此背鳍背缘在此形成一个浅的凹缺。最长鳍棘不短于鳍条。背鳍支鳍骨在已修理的标本中仅见17根，第一支鳍骨仅支持一根鳍棘。背鳍前方有三根背鳍前骨，背鳍前骨式(predorsal formula，据 Ahlstrom *et al.*，1976)在大多数标本中为 0/0/0 + 1/，即第一背鳍前骨位于第一躯椎神经棘之前，第二背鳍前骨位于第一、二躯椎神经棘之间，第三背鳍前骨和第一背鳍支持骨同位于第二和第三躯椎的神经棘之间，第一背鳍支持骨支持一根鳍棘。在采自三板桥的标本中我们也看到过可能是 /0+ 0/0/1 + 1/ 或 0/0/0/1 + 1/ 的情况(V11367.14)，这一标本的第一躯椎神经棘恰位于第一背鳍前骨之下，因此很难辨认前面两个背鳍前骨的插入情况，这当然和化石保存情况有关。但第一、二鳍条支持骨却明显地位于第三、四躯椎神经棘之间。

臀鳍基短，约与背鳍软鳍部分相对，鳍式为 Ⅲ，7—8，第一鳍棘最短，第二鳍棘最粗壮。支鳍骨数约 9 根(V11367，V11367.14)，第一支鳍骨长大，一直延伸到脊柱附近，并载有二鳍棘(据 Johnson，1984 的表述)，Arratia (1982)则把这种情况描述为第一、二支鳍骨愈合或部分愈合。

尾鳍浅叉形，上、下叶较对称，鳍式为 I，8，7，I。尾鳍上、下主鳍条外侧各有短鳍条(procurrent rays)12 根(V11367.8)(图 4)。

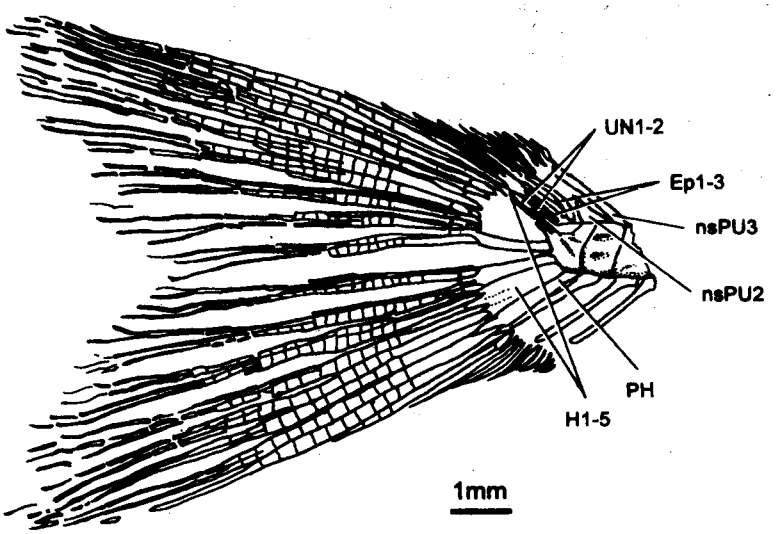

图4 秀丽洞庭鳜尾鳍及尾骨骼

Fig.4 *T. gracilis*, caudal fin and caudal skeleton, V11367.8

脊柱：脊椎骨 24—25 个，其中躯椎(abdominal)10—11 个，尾椎(caudal)14—15 个。椎骨侧面有一粗壮的纵脊，脊的上、下为长形凹坑。肋骨较粗壮，约 7 对。尾部骨骼为低等鲈形目鱼类中常见的型式(Wilson, 1977; Arratia, 1982; Johnson, 1984; Micklich, 1988a,b, 1989)。第一尾前椎(PU_1)和第一末端尾椎(U_1)愈合。无独立的第二末端尾椎(U_2)。尾神经骨(UN)2 枚，第一尾神经骨下部扩大成尾盖骨(stegural)。尾下骨(hypurals)5 枚，副尾下骨(parhypural)及第一、二尾下骨与尾鳍下叶鳍条相连，第三—五

尾下骨与尾鳍上叶鳍条相连。尾上骨(epurals)3枚。在大多数标本中第二尾前椎(PU_2)上的神经棘短，但在有些标本中这一神经棘和它前面几个脊椎上的神经棘一样长(图5)。

鳞片：颅顶后部、鳃盖骨、前鳃盖骨、下鳃盖骨、间鳃盖骨、部分眶下骨及其他颊部骨片均由圆鳞或栉鳞覆盖。体被栉鳞，鳞片的前部边缘较圆，自鳞片中心有4—5条向前延伸的放射纹，后部表面布满许多细小的、略呈放射状排列的栉，栉较短小，后端略钝(图版II,6)，这是否与标本的保存及修理情况有关，尚不能完全肯定。

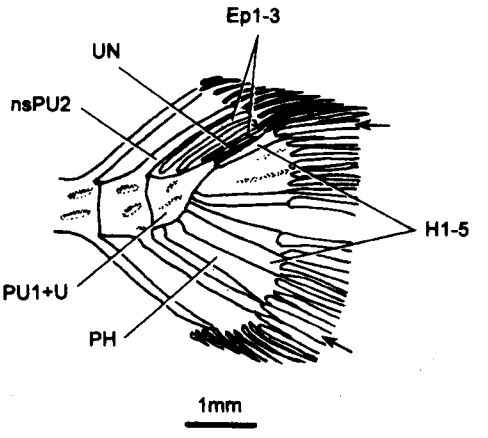

图5　秀丽洞庭鳜尾骨骼

Fig.5　*T. gracilis*, caudal skeleton, V11367.1

3　讨　论

3.1　洞庭鳜属的物种

自刘东生等(1962)发表秀丽洞庭鳜以来，已有5个种归入此属，包括产于湖南、广东的秀丽洞庭鳜，湖南的下湾铺洞庭鳜，江苏的洪泽洞庭鳜，安徽的来安洞庭鳜和山东的始新洞庭鳜。张弥曼等(1985)认为洞庭鳜可以分为湖南的一类和苏、皖的一类。本文记述的标本属于湖南的一类。

郑家坚(1962,340页)据以建立下湾铺洞庭鳜的理由是，它的前鳃盖骨上、下支相交不成直角，臀鳍基较长，有9根软鳍条，而秀丽洞庭鳜的前鳃盖骨两支间成直角，臀鳍基较短，只有7根软鳍条。根据我们对过去已有及新近采自湖南的洞庭鳜标本的观察，两个种的前鳃盖骨两支间的夹角实际上并无多大差别，都是大致成直角。臀鳍鳍条的数目在秀丽洞庭鳜和下湾铺洞庭鳜两个种的标本中都有8根，在三板桥的秀丽洞庭鳜标本中多为7根，而在下湾铺洞庭鳜的标本中多为9根，衡南的V5603中则为8根。背鳍式在三板桥的标本中为Ⅷ—Ⅸ，8—10，在下湾铺的标本中为Ⅸ—X，10，而在衡南标本V5603中为X，11，鳍条数目的差别都很有限(见表1)。现生鲈形目鱼类中，同一种的不同个体间鳍条数目的差别是很普通的事，如*Coreoperca herzi*的背鳍式为Ⅺ—XV，11—15(周才武等，1988)。

我们最近的观察发现，下湾铺洞庭鳜的鳞片和V5603的比较相似，都具有细长、致密且后端尖的栉，栉在鳞片上着生的范围较大(图版II,7,8)，而秀丽洞庭鳜鳞片的栉短而钝，栉的着生范围较小(图版II,6)。背鳍前骨式在三板桥的秀丽洞庭鳜的绝大多数标本中是0/0/0 + 1/，第一支鳍骨上只有一棘。下湾铺的V1105的背鳍前骨式为0/0/0 + 2/，V1105.1，V1105.3中也可能是同样的情况。衡南的V5603的背鳍第一支鳍骨肯定载有二根鳍棘，但由于该标本第二躯椎的神经棘保存很差，尚不能肯定它的位置确在第二和第三背鳍前骨之间，不过，估计这种情况的可能性很大，因此，它的背鳍前骨式很可能也是

0/0/0 + 2/ (见表 1)。虽然 Micklich(1988a, p.308)在讨论 *Bilinia uraschista* 的背鳍前骨及第一支鳍骨的插入方式时曾指出,在不同种或甚至同一种的不同个体间可能出现不同的情况,因此在同一种中可以看到不同的背鳍前骨式,但背鳍第一支鳍骨所支持的鳍条数目在同一种中是相同的。现生的 *Coreoperca* 属中,第一支鳍骨载有不同数目鳍棘的现象只出现在不同的种中,如在 *C. herzi* 中为 0/0/0 + 2, *C. whiteheadi* 及 *C. kawamebari* 中则为0/0/0 + 1(刘焕章、陈宜瑜,1994)。此外,秀丽洞庭鳜尾鳍主鳍条外侧短鳍条为 12 根,而下湾铺洞庭鳜及 V5603 中则为 7 根。因此,根据上面提到的背鳍前骨式、栉的形状和尾鳍主鳍条外侧短鳍条数目,下湾铺种应该是可以成立的。它和秀丽洞庭鳜的主要区别是,背鳍前骨式为 0/0/0 + 2/ ,鳞片的栉十分细长且末端尖,栉在鳞片上的着生范围较大,尾鳍主鳍条外侧短鳍条 12 根。秀丽洞庭鳜的背鳍前骨式为 0/0/0 + 1/,鳞片的栉短而钝,栉的着生范围较小,尾鳍主鳍条外侧短鳍条 7 根。在这一前提下,衡南的 V5603 标本(图 6)似应属于下湾铺洞庭鳜,而不是秀丽洞庭鳜。当然,三板桥标本鳞片上的栉较另外两地标本中的短小或许与保存和修理情况不无关系,加之,下湾铺的标本数量不多,衡南的标本只有一件,我们到湖南进行野外工作时虽特意造访了衡南龙湾滩采石场,无奈采石场已完全坍塌,且杂草丛生,无法进行采集。下湾铺洞庭鳜这一物种的成立以及产出它的地点还有待更多的信息来确认。我们最近看到的下湾铺洞庭鳜、秀丽洞庭鳜和产自衡南龙湾滩的 V5603 标本中上枕脊的上缘都增厚,同时也都有上枕骨骨架,则是它们共同的特征。

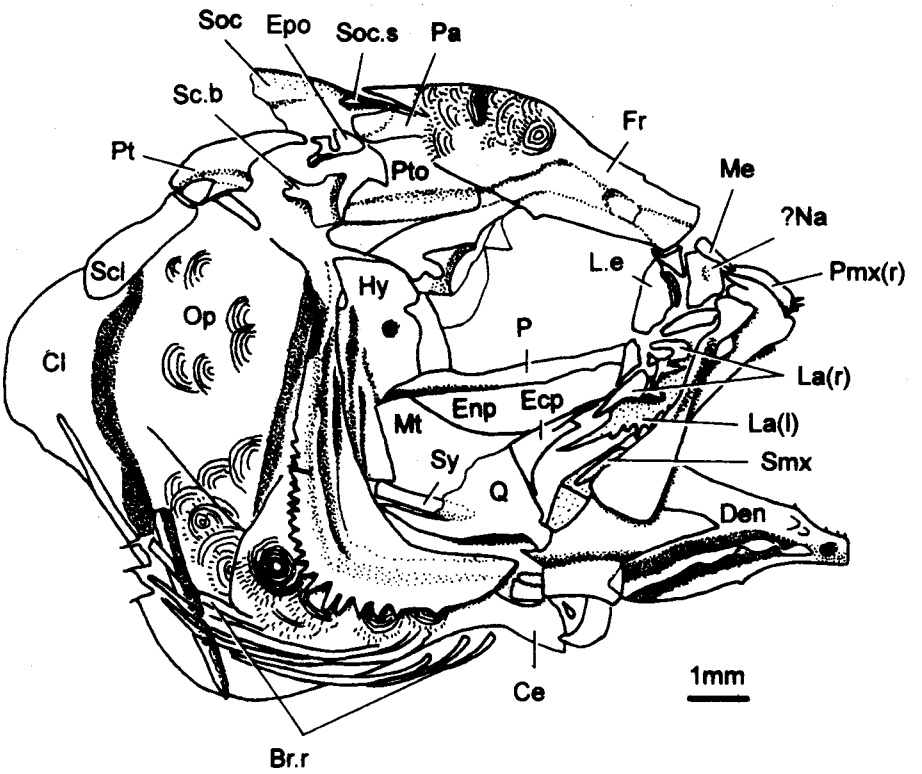

图6 V5603头骨右侧视

Fig.6 Possible *T. hsiawanpuensis*, skull in right view

此外，我们还观察到，下湾铺洞庭鳜的正型标本 V1105 的后颞骨后缘有细锯齿，这在其他众多的标本上还没有看见过。这一情况和鳍条数目的少量差别以及背鳍前骨和支鳍骨插入情况的不同，可能只是个体变异。*Priscacara liops* 的前鳃盖骨后缘有从具细锯齿到光滑的状态(Grande, 1984)。*Percichthys* 中前鳃盖骨、鳃盖骨、下鳃盖骨、间鳃盖骨、后颞骨、泪骨、眶下骨等边缘均具齿则当别论。*Amphiperca* 中背鳍前骨和背鳍支持骨的插入情况在同一种的不同个体间也有差别。三板桥的秀丽洞庭鳜的背鳍前骨和支持骨的插入情况以及尾骨构造中第二尾前椎上神经脊的长短和尾神经骨的数目在不同标本中都有所不同。这些事实表明，一些特征在早期低等鲈形目鱼类中有较大变异，存在多态性，它们的系统学意义还有待进一步认识。

表1　秀丽洞庭鳜、下湾铺洞庭鳜和衡南标本V5603的部分特征比较

Table 1　Comparison between *Tungtingichthys gracilis, T. hsiawanpuensis* and V5603 from Hengnan

种类 taxa	秀丽洞庭鳜 *Tungtingichthys gracilis*	下湾铺洞庭鳜 *Tungtingichthys hsiawanpuensis*	V5603
产地 locality	临澧三板桥 Sanbanqiao, Linli county	湘乡下湾铺 Xiawanpu, Xiangxiang county	衡南龙湾滩 Longwantan, Hengnan county
背鳍式 dorsal fin rays	VIII–IX, 8–10	IX–X, 10	X, 11
臀鳍式 anal fin rays	III, 7–8	III, 8–9	III, 8
后颞骨后缘锯齿 serration on posterior margin of posttemporal	未见 no	有 present	未见 no
鳞片栉的形式及着生范围 ctenii and area carrying them	栉短，后端钝；着生范围较小 short, posterior end blunt; area carrying ctenii small	栉细长，后端尖；着生范围较大 long and thin, posterior end pointed;area carrying ctenii large	栉细长，后端尖；着生范围较大 long and thin, posterior end pointed;area carrying ctenii large
背鳍前骨式 predorsal formula	0/0/0+1/	0/0/0+2/	0/0/0+2/
尾鳍主鳍条外侧短鳍条 procurrent rays	尾柄上、下各12根 12 on either side of caudal peduncle	尾柄上、下各7根 7 on either side of caudal peduncle	尾柄上、下各7根 7 on either side of caudal peduncle

3.2　洞庭鳜的属征

刘东生等(1962)、张弥曼等(1985)所提供的洞庭鳜的属征包括了他们当时在洞庭鳜标本中能够观察到的主要特征，其中许多在其他低等鲈形目鱼类中也能见到，并非洞庭鳜所特有。不过，在鲈形目鱼类系统发育情况还很不清楚，现代以及化石鲈形目鱼类的形态学研究还很不充分，而我们对世界各地各种化石鲈形目鱼类了解还很不够的情况下，要确定洞庭鳜(或任何一个低等鲈形目鱼类的属)的属征是一件十分困难的事。我们在对标本重新采集、修理、观察的基础上，对洞庭鳜的骨骼形态作了补充描述，并和欧洲及美洲同时代的早期鲈形目鱼类代表种类(德国 Darmstadt 附近 Messel 中始新世油页岩组 [Oilshale Formation]的 *Amphiperca*，美国怀俄明州中始新世绿河页岩 [Green River Shales]、加拿大 British Columbia 的 Horsefly 地点的 *Priscacara* 和南美现生的 *Percichthys* 以及此属在阿根廷和智利安第斯山脉早第三系地层中的代表)作了比较(见表 2)。从表 2 中列出的情况来

表2 *Tungtingichthys, Amphiperca, Priscacara* 和 *Percichthys* 特征比较

Table 2 Comparison between *Tungtingichthys, Amphiperca, Priscacara* and *Percichthys*

taxa	*Tungtingichthys*	*Amphiperca*	*Priscacara*	*Percichthys*
大小 size	最大体长 maximum standard length 63mm	大于洞庭鳜 larger than *Tungtingichthys*	最大全长 maximum total length 380 mm (*P. serrata*); 150mm (*P. liops*)	最大全长 total length 110 cm (*P. hondoensis*); 70—77mm (*P. lonquimayiensis*); 70mm (*P. sandovali*)
体高/体长 body depth/standard length	27%—38%	45%—50%	42%—59%	27%—33%
上枕脊上缘 upper margin of supraoccipital crest	加厚 thickened	加厚 thickened	?	加厚 thickened
上枕骨架 supraoccipital shelf	有 present	有 present	?	有 present
下颌关节 articulation of lower jaw	位于眼眶中点之前 anterior to midline of orbit	位于眼眶中点之后 posterior to midline of orbit	位于眼眶中点之前 anterior to midline of orbit	口裂中等大小 mouth moderate in size
辅上颌骨 supramaxilla	有 present	有 present	?	有 present
鳃盖骨后缘具棘 spines on posterior margin of opercular	1	2	3 or 4 (*P. aquilonia*)	2
前鳃盖骨后缘及下缘 posterior and ventral margin of preopercular	有锯齿 serrated	有锯齿 serrated	有锯齿 serrated (*P. serrata*); 锯齿极细微或边缘平滑 finely serrated or smooth (*P. liops*)	有锯齿 serrated
泪骨下缘 ventral margin of lachrymal	有锯齿 serrated	平滑 smooth	?	有锯齿 serrated
其他眶下骨下缘 ventral margin of other cheek bones	未见锯齿 not serrated	未见锯齿 not serrated	未见锯齿 not serrated	有锯齿 first and second infraorbitals serrated

续表2

taxa	*Tungtingichthys*	*Amphiperca*	*Priscacara*	*Percichthys*
后颞骨后缘 posterior margin of posttemporal	平滑或有细微锯齿 smooth or finely serrated	平滑 smooth	?	有锯齿 serrated
鳃条骨 branchiostegal rays	6	6	6	6
咽齿 pharyngeal teeth	臼状 molariform	臼状 molariform	臼状 molariform	尖 pointed
背鳍前骨 predorsal	3	3	3	3
胸鳍条 pectoral fin rays	13—15	15	12—15(*P. liops*)	11—14 (*P. hondoensis*); 15—16 (*P. lonquimayiensis*)
腹鳍条 pelvic fin rays	I, 5	I, 5	I, 5—6 (*P. liops*)	I, 5
背鳍鳍基部分和鳍条部分 spinous and soft-ray parts of dorsal fin	连续 continuous	连续 continuous	连续 continuous	基部连续 joined at base
鳍棘部分基部 base of spinous part	长于鳍条部分基部 longer than base of soft-ray part	与鳍条部分基部约等长 as long as base of soft-ray part	长于鳍条部分基部 longer than base of soft-ray part	长于鳍条部分基部 longer than base of soft-ray part (measured from Arratia, 1982, fig.113)
背鳍最长鳍棘 longest spine of dorsal fin	不短于鳍条 longer than soft rays	短于鳍条 shorter than soft rays	不短于鳍条 longer than soft rays	不短于鳍条 longer than soft rays
背鳍中部凹刻 cleft in middle of dorsal fin	浅 shallow	浅 shallow	浅 shallow	深 deep
背鳍前骨式 predorsal formula	0/0/0+1/ or 0/0/0+2/	0/0/0+2/	0/0/0+2/ (counted from fig. II.88, 89, 91—93, Grande, 1984)	0-0-0-1-(*P. hondoensis, P. lonquimayiensis*); 0-0-0-2-(*P. sandovali*)
背鳍式 dorsal fin rays	Ⅷ—Ⅹ, 9—11	Ⅸ—Ⅹ, 12	Ⅹ, 9—10 (*P. serrata*); Ⅹ, 12—13 (*P. liops*)	ⅩⅢ—Ⅹ, 12 (*P. hondoensis*); Ⅺ, 10 (*P. lonquimayiensis, P. sandovali*)

续表2

taxa	*Tungtingichthys*	*Amphiperca*	*Priscacara*	*Percichthys*
臀鳍式 anal fin rays	III, 7—9	III, 8—9	III, 8—9 (*P. serrata*); III, 10—12 (*P. liops*)	III, 7—8 (*P. hondoensis*); III, 10 (*P. lonquimayiensis*); III, 9 (*P. sandovali*)
臀鳍第一支鳍骨 first pterygiophore of anal fin	长且粗壮，具2棘 long and robust, with 2 spines	长且粗壮，具2棘 long and robust, with 2 spines	长且粗壮，具2棘 long and robust, with 2 spines	长且粗壮，具2棘 long and robust, with 2 spines
尾鳍主鳍条 main caudal fin rays	I, 8, 7, I	I, 8, 7, I	I, 8, 7, I	I, 8, 7, I
尾鳍主鳍条外侧短鳍条 procurrent rays	尾柄上、下各7或12根 7/12	?	?	尾柄上、下各13根 13 (*P. sandovali*)
尾鳍后缘 shape of caudal fin	浅叉形或截形 slightly forked or truncated	略呈圆形 rounded	略凸圆 slightly rounded convexly	浅叉形 slightly forked
第一尾前椎及第一末端尾椎 PU_1 and U_1	愈合 fused	愈合 fused	愈合 fused	愈合 fused
独立的第二末端尾椎 independent U_2	无 absent	无 absent	无 absent	无 absent
尾上骨 epurals	3	3	3 (*P. aquilonia*)	3
尾下骨 hypurals	5	5	5 (*P. aquilonia*)	5
尾神经骨数目 number of UN	2 (包括尾盖骨) 2, including stegural	无单独的第二尾神经骨 no independent UN_2	2 (包括尾盖骨) 2, including stegural (*P. aquilonia*)	2 (包括尾盖骨) 2, including stegural (*P. sandovali*)
第二尾前椎神经脊 neural spine on PU_2	通常低，在少数具2尾上骨的标本中长 usually low, long in a few specimens with 2 EPs	低 low	低 low	低 low
椎骨 vertebrae	24—25 (10—11+14—15)	26—27 (10—11+16—17)	25—27 (10—12+14—15)	30—32 (*P. lonquimayiensis*, *P. sandovali*) (13/14—17/18)
鳞 scales	栉鳞，颅顶后部及颊部均被鳞 ctenoid, posterior portion of skull roof and cheek covered with scales	栉鳞，颅顶后部及颊部均被鳞 ctenoid, posterior portion of skull roof and cheek covered with scales	栉鳞，鳃盖骨被鳞 ctenoid, opecular covered with scales	栉鳞 ctenoid

看，很难确认任何一个属的特有离征(autapomorphies)。几乎目前在洞庭鳜中观察到的全部特征在另外三个属或其中一、二属中都可以看到。例如洞庭鳜鱼体较小，体较低，泪骨下缘有较大的锯齿，个别标本中后颞骨后缘亦有细锯齿，尾鳍后缘呈浅叉形等等虽不同于*Amphiperca*和*Priscacara*，但这些特征在*Percichthys*中都可以看到。另一些不同于*Percichthys*的特征，如背鳍背缘的凹刻较浅，椎骨数目较少，上、下咽骨具臼状齿等，却又与*Amphiperca*及*Priscacara*共有。因此，我们还远不能说这些就是洞庭鳜的属征。另一种情况是，洞庭鳜的另一些特征，在其他一些属中情况不明，如上枕脊上缘加厚，有上枕骨骨架，有辅上颌骨等，在*Priscacara*中的情况不明。根据我们观察，洞庭鳜鳃盖骨后缘具一棘，*Amphiperca*具二棘(Micklich, 1987)，绿河页岩中的*Priscacara*的描述中虽然没有提到鳃盖后缘的构造，但加拿大British Columbia的*P. aquilonius*的鳃盖后缘是有3或4个棘的(Wilson, 1977)。对于这些特征我们掌握的信息不全，也很难作出恰当的评价。世界其他地区早期鲈形目鱼类的研究者在确定属征时恐怕也遇到同样的问题，例如，Arratia(1982)所提供的*Percichthys*的属征和Micklich(1987, p.55)所提供的*Amphiperca*的属征也大多是它们的总体特征，其中包含了许多其他低等鲈形目鱼类中普遍存在的特征。至于说到*Priscacara*，到目前为止，我们还没有看到有关此属的详细描述，Cope(1877, 1884)提出的属征也只是他当时所能观察到的*Priscacara*的总体性状，并非*Priscacara*所特有，而Grande(1980, p.149—151)只提供了有关此属的一些基本资料。在这种情况下，我们仍只能暂将观察到的洞庭鳜的主要特征归结为它的属征(见上文属征)，其中也包括了低等鲈形目鱼类所共有的特征。究竟哪些是洞庭鳜真正的属征，尚需在鲈形目的系统分类有了眉目以后才能确定。虽然如此，经过对较多标本的进一步修理和观察，我们的属征中增加了一些过去没有观察到的重要特征，也纠正了过去观察中的一些错误，使我们对洞庭鳜骨骼学的认识比以前更进了一步。

3.3 洞庭鳜属的系统位置

刘东生等(1962)曾将洞庭鳜归入射水鳜科(Toxotidae)。夏树芳等(1979)、张弥曼等(1985)又将洞庭鳜归入鮨科(Serranidae)。这里的鮨科是传统意义上的鮨科，是将别的类群独立出去后剩下的低等鲈形目鱼类的一个混合体。近年来，在对现生鲈形目鱼类系统学的研究中，传统意义上的鮨科含义发生了变化，仅指原来鮨科中鳃盖骨后缘有三根棘的种类(Gosline, 1966)，其他类群则被排除出去，部分被归入Percichthyidae科，部分成为其他一些科的成员，还有一些系统位置难以确定。从洞庭鳜属所具有的特征看来，它也是一个系统位置难以确定的属。

世界各地其他始新世低等鲈形目鱼类的归属也是一个悬而未决的问题。北美的*Priscacara*曾被不同作者先后归入现生科Pomacentridae(Cope, 1884; Woodward, 1901)，Cichlidae(Haseman, 1912)，Centrarchidae(Regan, 1916)，而Jordan(1923)为它特意建立了一个化石科Priscacaridae。关于Messel的始新世低等鲈形目鱼类如*Amphiperca*等，Micklich(1987)则将其归入Serranidae/Percichthyidae这一类群，而目前公认的这两个科都不是单系类群。

Cavender(1986)在讨论北美淡水鱼类化石历史时，将北半球现生的鲈形目鱼类*Morone*，*Lateolabrax*以及只分布于中国、朝鲜、越南北部淡水水域中的*Siniperca*等都归

入 Percichthyidae 科，同时他也将北美绿河页岩中的鲈形目鱼类如 *Priscacara* 等归入此科。在 Percichthyidae 一节中他提到了欧洲中始新世包括 *Amphiperca* 在内的一些鲈形目鱼类，也提到了中国的洞庭鳜，虽然他并未将这些鱼类明确地归入此科而仅称它们为原始鲈亚目化石 (primitive percoid fossils)。不过，许多研究者都认为 Gosline(1966) 所界定的 Percichthyidae 不是一个自然类群 (Arratia, 1982) 而是一个复系类群 (Johnson, 1984)，后者并认为此科应仅包括产于南美及澳洲淡水中的属。

洞庭鳜和 *Amphiperca, Priscacara, Percichthys* 共有许多特征，包括鳍、背鳍前骨、鳃条骨、尾骨骼基本构造、椎骨数目、鳞片类型等 (见表 2)。这些特征中的绝大部分正是 Johnson(1984, p.473—484, Table 120) 所列出的鲈亚目 (Percoidei) 成年个体中最常见的特征，或者可以说是鲈亚目的原始特征。如：腹鳍具 1 鳍棘 5 鳍条；尾鳍主鳍条 9+8根，尾鳍主鳍条外侧短鳍条通常为 8—14 根；背鳍的鳍棘部分与鳍条部分连续，两部分间有不同程度的凹刻，最后一根鳍棘长于倒数第二根鳍棘并构成背鳍鳍条部分的第一成分；臀鳍具三鳍棘，第一支鳍骨大，载有二鳍棘 (或如 Arratia[1982] 所表述：第一、二支鳍骨愈合或部分愈合)；背鳍前骨 3 根，第一支鳍骨插入第二、三神经棘间隔，通常载有二棘，最常见的背鳍前骨式为 0/0/0+2/ 及 0/0+0/2/；尾骨骼具 5 根尾下骨、2 根尾神经骨、3 根尾上骨、一个末端尾椎 (由第一尾前椎和一或二个末端尾椎愈合而成)、第二尾前椎上的神经棘低，第一、二及第三、四尾下骨常愈合，第二根尾神经骨常缺失；椎骨数通常为 24—27 个等 (Johnson, 1984)。但这些特征恐怕也是整个鲈形目的原始特征。正如许多作者所说，鲈亚目这个真骨鱼类中最大的亚目和鲈形目一样，都是至今尚未找到合适离征来界定的类群，很可能是复系的类群 (Gosline, 1966; Johnson, 1984, 1993)。因此，讨论这几个属是否可以归入鲈亚目的问题实际上是没有意义的。

洞庭鳜，*Amphiperca* (Micklich, 1987) 及 *Priscacara* (Haseman, 1912; Jordan, 1923; Rosen and Patterson, 1990) 都具有臼状咽齿，这也是 Haseman 将 *Priscacara* 置于 Cichlidae 以及 Jordan 将它归入属于咽颌类 (Pharyngognathi) 中的 Chromides 的理由之一。咽骨具有臼状咽齿，或称咽颌 (Pharyngognathy)，即第五对角鳃骨增大并具臼状齿，同时，与其相对的几个咽鳃骨具齿板。在许多种类中左右两个角鳃骨在中线愈合形成一个三角形的硕大骨片，但在个别种类如 cichlids 中左、右下咽骨并不愈合。咽颌在鲈形目鱼类中的分类意义曾经引起过许多讨论。上一世纪的鱼类学家如 Müller(1846) 等将现生棘鳍鱼类 (Acanthopterygii) 中具有臼状咽齿的种类归入咽颌类，但后来的许多鱼类学家如 Regan(1929)、Berg(1940) 等则认为咽颌是一种趋同或平行进化，而将具有臼状咽齿的种类归入不同类群中。不少新近的研究者如 Kauffman 和 Liem(1982) 以及 Stiassny 和 Jensen(1987) 等通过分支系统学研究又重新将咽颌及其他与其相关的特征视作共有离征而将大部分具咽颌的棘鳍鱼类归入一个广义的隆头鱼亚目 (Labroidei) 中。不过，Johnson(1993) 等人并不同意这一观点，他认为，Stiassny 和 Jenson(1987) 确定广义的隆头鱼亚目为单系类群的证据都集中在咽部，鱼体骨骼的其他方面并未提供任何近缘的线索，而且 Stiassny 和 Jenson 所提出的八个咽部的共有离征并非隆头鱼亚目所特有，所有这些与咽部有关的特征都能在与它们无近缘关系的棘鳍鱼类中找到，同时，也并非隆头鱼亚目的全体成员都具有这八个特征。因此，到目前为止，咽颌能否用作共有离征或仅是非同源相似 (homoplasy) 还不是一个已经完全解决了的问题。对

于化石种类洞庭鳜、*Amphiperca* 和 *Priscacara* 来说，情况就更困难，因为我们虽然看到它们的臼状咽齿，但除了在 *Priscacara* 中观察到虽愈合但仍具中缝的下咽骨(Haseman, 1912)外，在其他种类中并没有清楚地看到咽骨，更无法辨认左右下咽骨是否愈合成一个整体。值得提到的是，*Percichthys* 是没有臼状咽齿的(据 Arratia 告知)，这或许是它和上面提到的北半球的几个化石鲈形目鱼类的一个重要区别。

除臼状咽齿外，北半球的几个属还共有几个在 *Percichthys* 中不存在的特征，即椎体少于 30 枚，背鳍鳍棘部分和鳍条部分间的凹刻比 *Percichthys* 的要浅得多，眶下骨下缘无锯齿。从北半球的几个属所共有而 *Percichthys* 不存在的特征来看，北半球的几个属之间的关系似比它们和 *Percichthys* 的关系要来得近。北半球始新世的几个化石属归入 Percichthyidae 科看来是没有足够根据的。至于说到欧洲、亚洲和北美始新世化石鲈形目鱼类之间的亲疏，则需在对更多化石的更深入的研究后，甚至要等到现生低等鲈形目鱼类的系统关系基本确立之后才能得出比较肯定的结论。

4 结　论

1) 湖南省境内始新世洞庭鳜与世界各地同时代以及现代低等鲈形目鱼类的骨骼构造共有很多鲈形目的原始特征。它的许多其他特征在低等鲈形目鱼类的各种类群中也有不同程度的分布，但总的确切分布情况尚不甚明了。

2) 湖南省境内现有的两种洞庭鳜，即秀丽种和下湾铺种，在背鳍前骨式、鳞片上栉的形状和分布范围以及尾鳍主鳍条前的短鳍条数目方面有显著差异。基于这些区别，这两个种是可以成立的。根据上述标准，张弥曼等(1985)归入秀丽种的 V5603 标本应归入下湾铺种而不是秀丽种。

3) 从洞庭鳜，欧洲的 *Amphiperca*，北美的 *Priscacara* 以及南美的 *Percichthys* 的比较来看，北半球的几个属之间比它们与南美的 *Percichthys* 更接近，因此，将北半球的几个化石属也一并归入 Percichthyidae 科的做法看来并不妥当。由于对上述化石种类的研究尚欠充分，目前还不可能讨论北半球几个地区的种类间关系的亲疏。

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REEXAMINATION OF *TUNGTINGICHTHYS* (PISCES, PERCIFORMES) FROM HUNAN PROVINCE, CHINA

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Key words　*Tungtingichthys*, Eocene, redescription, comparison

Summary

The Eocene perciform *Tungtingichthys* has been found widely spread over eastern and southern China. Since the genus was first established by Liu *et al.* (1962), five species (*T. gracilis, T. hsiawanpuensis, T. laianensis, T. hongzeensis,* and *T. eocaenus*) have been described from Hunan, Anhui, Jiangsu, Guangdong, Shandong and Liaoning Provinces (Fig. 1). Most of the specimens are preserved in oil shale and are very difficult to prepare and for this reason previous descriptions are in many ways incomplete. The purpose of this paper is to redescribe the type species of the genus, *T. gracilis,* based on newly prepared specimens collected from Hunan Province, to review their systematics and to compare *Tungtingichthys* with contemporaneous perciforms from other continents. The specimens used in this study include those from the collections of the IVPP and those newly collected by the senior author and her colleagues in 1991 from the type locality of the type species, i.e. Sanbanqiao (village), Shimen (town), Linli county, Hunan Province. After trying different ways of preparation with no success most of specimens are prepared mechanically with a thin needle. One of them (V11367) is prepared by transfer method.

1 Systematics

Superoder Percomorpha Rosen, 1973

Order Perciformes Regan, 1913

Suborder and family indet.

***Tungtingichthys* Liu *et al.* 1962**

Revised diagnosis Small fish with relatively low body depth, laterally compressed, known maximum standard length 63 mm, body depth consisting 27%— 38% of standard length; upper margin of supraoccipital crest thickened, supraoccipital shelf present; orbit comparatively large, its diameter longer than antorbital distance, mouth terminal or slightly supraterminal, mouth margin of premaxilla and dentary covered by fine teeth, premaxilla with ascending and articular processes, tiny supramaxilla present, palatine with small teeth; opercular with one spine, preopercular finely serrated posteriorly while its ventral margin with fewer and broader serrations; branchiostegal rays 6; ventral margin of lachrymal prominently serrated; upper and lower pharyngeals with molariform teeth; spine part of dorsal fin continuous with soft-ray part, base of former longer than that of latter, dorsal margin slightly notched between two parts, last spine longer than preceding one, D VIII—X, 8—11; predorsal formula in *T. gracilis* 0/0/0+1/, in *T. hsiawanpuensis* 0/0/0+2/; A III, 7—9; P 13—15; V I, 5, caudal fin slightly forked, PU_1 fused with U_1, no independent U_2, hypurals 5, uroneurals 2, anterior portion of UN_1 enlarged to form stegural, epurals 3, neural spine on PU_2 in most of specimens short, in very few specimens long; vertebrae 24—25; scales on body ctenoid, posterior portion of skull roof and cheek covered with cycloid or ctenoid scales.

***Tungtingichthys gracilis* Liu, Liu et Tang, 1962**

Revised Diagnosis Predorsal formula 0/0/0+1/; dorsal spines VIII in most specimens, very rarely IX, soft rays of anal fin 7—8; ctenii on scale short and blunt; procurrent rays 11—12.

Locality, horizon and age Sanbanqiao, Shimen, Linli county, Hunan Province; Xiejiashan Formation, Eocene.

The full description of *T. gracilis* is not presented in the English summary. For the main characters see Tab. 1, 2; Figs. 2—6 and Pl. I, II.

2 Discussion

Since the description of *T. gracilis* by Liu *et al.* (1962) four more species were added to the genus (see above). While describing *T. eocaenus* Chang *et al.* (1985) noticed that those from Hunan Province and those from Jiangsu and Anhui Provinces differ in many ways and might finally be subdivided into two groups. The discussion

here involves only those from Hunan.

2.1 Validity of *T. hsiawanpuensis*

The diagnostic characters suggested by Cheng (1962,p. 340) for *T. hsiawanpuensis* are: the two arms of the preopercular form a right angle; the anal fin contains nine soft rays and thus forming a slightly longer base than that of *T. gracilis*. According to our observation the angle between the two arms of the preopercular is more or less the same, i.e. roughly a right angle, in the two species. The number of the anal soft rays in *T. gracilis* is 7—8, in *T. hsiawanpuensis* is 8—9 while in V5603 from Hengnan it is 8. So these two characters are not diagnostic. Besides, the number of the dorsal fin rays are also inconsiderable (VIII—IX, 8—10 in *T. gracilis*, IX—X, 10 in *T. hsiawanpuensis* and X, 11 in V5603, see Tab. 1). It is common in Recent perciforms that the number of fin rays varies in different individuals of the same species. For instance, the dorsal fin rays in *Coreoperca herzi* are XI—XV, 11—15 (Zhou *et al.*, 1988).

Our current observation, however, reveals quite a few distinctions between *T. gracilis* and *T. hsiawanpuensis*. In the former species the scales bear short and blunt ctenii and the area for attachment of ctenii is narrow. In the latter species as well as in V5603 the ctenii are long and pointed and the area for attachment of ctenii is broader (Pl. II, figs. 6—8). The predorsal formula in most specimens of *T. gracilis* is 0/0/ 0+1/ while in *T. hsiawanpuensis* V1105, V1105.1 and V1105.3 it is 0/0/ 0+2/. Though the neural spine of the second vertebra is badly preserved in V5603 and we are not sure whether it is situated between the second and third predorsals as it is in *T. hsiawanpuensis*, one fact is certain that the first pterygiophore of the dorsal fin in this specimen carries two short spines. While discussing about the insertion of the first dorsal pterygiophore between the neural spines in *Bilinia uraschista* Micklich (1988a, p. 308) mentioned that though the situation varies in different species of the same genus or even in different individuals of the same species the number of the fin spines carried by the first dorsal pterygiophore remains constant in the same species. The same relation can be seen in Recent perciforms. For instance, in *Coreoperca* the number of fin spines carried by the first dorsal pterygiophore varies only in different species. The predorsal formula in *C. herci* is 0/0/0+2/ while in *C. kawamebari* and *C. whiteheadi* it is 0/0/0+1/ (Liu *et al.* 1994). Besides, the number of procurrent rays in *T. gracilis* is approximately 12 whereas in V5603 and *T. hsaiwanpuensis* it is around 7. Thus, *T. hsaiwanpuensis* can easily be distinguished from *T. gracilis* by the predorsal formula (0/0/ 0+2/), fine, long and pointed ctenii, broader attachment area for ctenii and bigger number of procurrent rays (12) (see Tab. 1) and is, therefore, a valid species. In this case, the specimen V5603 from Hengnan should rather be referred to *T. hsaiwanpuensis* than to *T. gracilis*.

We also observed, the posterior border of the posttemporal of the holotype of *T. hsaiwanpuensis* V1105 is finely serrated while in all other specimens of *Tungtingichthys* it is smooth. This condition and the slight differences in the number of fin rays and insertion of predorsals and pterygiophores between neural spines of vertebrae are probably just individual variations. The posterior margin of the preopercular in different individuals of *Priscacara liops* can also be seen from finely serrated to smooth (Grande, 1984). The insertion of predorsals and pterygiophores varies in different individuals of the same species of *Amphiperca*. In *T. gracilis* from Sanbanqiao the insertion of predorsals and pterygiophores, the length of the neural spine of PU_2 and the number of uroneurals varies in different individuals. These facts show that some characters in early perciforms have considerable range of variation yet the phylogenetic implication of them is still awaiting further investigation.

2.2 Diagnosis of *Tungtingichthys*

The diagnoses of *Tungtingichthys* provided by Liu *et al.* (1962) and Chang *et al.* (1985) incorporate the main characters they noticed from the specimens of the genus. Many of them are not only present in *Tungtingichthys* but also in other lower perciforms. It is, in fact, a very hard task to set a diagnosis for *Tungtingichthys* (or for any other genus of lower perciforms) when the phylogeny of Recent perciforms is not well-established and the knowledge of morphology of fossil perciforms is inadequate. Based on our examination of newly collected and prepared specimens additional description of the osteology of *Tungtingichthys* and comparison with some of the contemporaneous forms from Europe and America (*Amphiperca* from the Middle Eocene Oilshale of Messel near Darmstadt, *Priscacara* from the Middle Eocene Green River shale of Wyoming, the United States and Horsefly, British Columbia, Canada and Recent *Percichthys* from South America and their fossil representatives from Paleogene of Argentine and Chili) are made (Tab. 2). Table 2 shows that nearly all characters seen in *Tungtingichthys* can be observed either in the other three genera or in one or two of them. It is very difficult to define autapomorphies for any of these genera. For instance, part of the characters of *Tungtingichthys*, e. g. small size, low body depth, comparatively gross serration on ventral margin of lachrymal, fine serration on posterior margin of posttemporal, slightly forked caudal fin etc. are not found in *Amphiperca* and *Priscacara* but they are all present in *Percichthys*. Other characters of *Tungtingichthys*, e. g. the shallow notch at dorsal margin of dorsal fin, less number of vertebrae, molar-like phayngeal teeth etc. are not seen in *Percichthys* but are shared with *Amphiperca* and *Priscacara*. Therefore, they are not diagnostic for *Tungtingichthys*. As for some other characters present in *Tungtingichthys*, e. g. thickened dorsal margin of supraoccipital crest, supraoccipital shelf, supramaxilla etc., there is no sufficient information in some of the other three genera. So it is difficult

to make appropriate judgement about them. The researchers on lower perciforms from other areas of the world have, perhaps, encountered the same problems. The diagnoses of *Percichthys* and *Amphiperca* given by Arratia (1982) and Micklich (1987) respectively are, on the whole, overall characters of these genera which include many characters present in other lower perciforms. As for *Priscacara,* no detailed description has been published so far. The diagnosis provided by Cope (1877, 1884) is actually the main characters he could observe in the specimens of *Priscacara* but not specific for it. Grande (1980, p. 55) provided some basic data for this genus. In this case, what we can do at present is to sum up all main characters we notice from the specimens of *Tungtingichthys* as its diagnosis (see diagnosis above) which includes a few characters shared by all lower perciforms. The proper diagnosis of *Tungtingichthys* can be made only when the phylogeny of Perciformes as a whole is done.

2.3 Phylogenetic position of *Tungtingichthys*

Liu *et al.* referred *Tungtingichthys* to Toxotidae. Xia *et al.* (1979) and Chang *et al.* (1985) later moved it to Serranidae in the traditional sense, i.e. as a mixture of lower perciforms. Serranidae recently is regarded as including only those who bear three spines at the posterior margin of their opercular (Gosline, 1966). The other forms are excluded. Part of them are transferred to Percichthyidae while some others are referred to other families. The rest remain incerti sedis. According to what we know about *Tungtingichthys* it can only be referred to the last case.

The phylogeny of the Eocene perciforms from other areas of the world is also unsettled. *Priscacara* from North America has been referred to the Recent families Pomacentridae (Cope, 1884; Woodward, 1901), Cichlidae (Haseman, 1912) and Centrarchidae (Regan, 1916). Jordan (1923) established a fossil family Priscacaridae specially for it. As for the Eocene perciforms from Messel, e.g. *Amphiperca* and others, Micklich (1987) refers them to a group of Serranidae/Percichthyidae though neither of the two families is accepted as monophyletic.

When discussing the history of North American fresh water fossil fishes, aside from the south hemisphere *Percichthys,* Cavender (1986) grouped the Recent perciforms *Morone, Lateolabrax* and *Siniperca* from North hemisphere into the family Percichthyidae as well. He also placed the fossil perciforms from Green River shale, e.g. *Priscacara* etc. in the same family. In the same passage, he mentioned the Middle Eocene perciforms *Amphiperca* and others from Europe and *Tungtingichthys* from China though he did not refer them to the family Percichthyidae. He just called them primitive percoid fishes. The distribution of the Chinese perch *Siniperca* is restricted to fresh water of East Asia, i.e. China, Korea and North Vietnam. Many workers suggest that Percichthyidae sensu Gosline (1966) is not a natural group (Arratia, 1982) but a polyphyletic one (Johnson, 1984). Johnson (1984) proposes the family to include

only genera from South America and Australia.

Tungtingichthys, Amphiperca, Priscacara and *Percichthys* share many characters (see Tab. 2). These characters are just those tabulated by Johnson (1984, p. 473—484, Table 120) as often seen in percoid adults or, we can say, they are primitive percoid characters. They are, perhaps, primitive characters for the whole Perciformes as well. Many authors suggested that Percoidei, the largest suborder in Teleostei, as Perciformes, is not defined by any synapomorphies and thus is also a polyphyletic group (Johnson, 1984, 1993; Johnson and Patterson, 1993). Therefore, to discuss whether the genera mentioned above belong to Percoidei is meaningless.

Tungtingichthys, Amphiperca (Micklich, 1987) and *Priscacara* (Haseman, 1912; Jordan, 1923; Rosen and Patterson, 1990) all have molar-like pharyngeal teeth. This is, perhaps, one of the reasons why Haseman referred *Priscacara* to Cichlidae and Jordan placed it to Chromides of Pharyngognathi. The phylogenetic implication of the pharyngognathy has long been an issue of dispute. Quite recently, through cladistic phylogenetic study, using pharyngognathy and other related characters as synapomorphies Stiassny and Jensen (1987) grouped most acanthopterygians with pharyngognathy into Labroidei (sensu lato). Johnson (1993) and others, however, do not agree with this point of view. Thus, whether pharyngognathy is a synapomorphy or just homoplasy remains so far unsolved. For the fossil forms, it is more difficult in this respect. We can see pharyngeal teeth in many specimens but except for fused pharyngeal bones with a median suture observed in *Priscacara* (Haseman, 1912) we have had no chance to see pharyngeal bones in any other forms, not speaking about whether the bones are fused or not. It is worth of mentioning that *Percichthys* does not have molar-like pharyngeal teeth (Arratia, pers. comm.). This is, perhaps, a character of some importance to distinguish the north hemisphere Eocene fossil perciforms from the southern one.

Aside from molar-like pharyngeal teeth the few Eocene perciforms share some other characters which are not found in *Percichthys*. These are: the vertebrae less than 30, the notch between the spine and soft ray parts of the dorsal fin shallower than that in *Percichthys*, the ventral margin of infraorbitals not serrated. Judging from these characters the north hemisphere forms seem more closely related than any of them with *Percichthys*. There is, so far, no sufficient ground to refer them to Percichthyidae. As for the relationships between the Eocene perciforms from Europe, Asia and North America it is pending further study of these fossil forms and a more or less certain phylogeny of the Recent perciforms.

3 Conclusions

1) *Tungtingichthys* from the Eocene of Hunan shares many perciform primitive

characters with its contemporaneous and Recent lower perciforms from other areas of the world. Its other characters are also shared in different extent by other perciform groups though the exact distribution of the characters is not yet clear.

2) The two previously described species of *Tungtingichthys, T. gracilis* and *T. hsiawanpuensis* are all valid. They can be distinguished in the predorsal formula, the shape and area of attachment of the ctenii and the number of the procurrent rays. According to these criteria the specimen V5603 from Hengnan should probably be referred to *T. hsiawanpuensis* but not to *T. gracilis*.

3) Judging from the comparison between *Tungtingichthys, Amphiperca, Priscacara* and *Percichthys* the genera from north hemisphere seem more closely related between themselves than with *Percichthys* from the south hemisphere. It is inappropriate to refer the fossil genera from north hemisphere to Percichthyidae. Due to inadequate study it is too early to discuss about the relationships between these fossil forms from north hemisphere.

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插图简字说明(Abbreviations used in figures)

Ang	angular	隅骨	Io	arts of infraorbital bones carrying sensory canal	眶下骨具感觉沟的部分
Art	articular	关节骨			
Br.r	branchiostegal rays	鳃条骨	Iop	interopercular	间鳃盖骨
Ce	ceratohyal	角舌骨	La	lachrymal	泪骨
Cl	cleithrum	匙骨	L.e	lateral ethmoid	侧筛骨
Den	dentary	齿骨	Me	methethmoid	中筛骨
Dsp	dermosphenotic	膜质蝶耳骨	Mx	maxilla	上颌骨
Ecp	ectopterygoid	外翼骨	Mt	metapterygoid	后翼骨
Enp	entopterygoid	内翼骨	Na	nasal	鼻骨
Ep	epural	尾上骨	nsPU$_2$	neural spine of PU$_2$	第二尾前椎神经棘
Epo	epiotic	上耳骨	nsPU$_3$	neural spine of PU$_3$	第三尾前椎神经棘
Fr	frontal	额骨	Op	opercular	鳃盖骨
H	hypural	尾下骨	P	parasphenoid	副蝶骨
Hy	hyomandibular	舌颌骨	Pa	parietal	顶骨

Pal	palatine	腭骨	Sc.b	scale bone	鳞片骨
PH	parhypural	副尾下骨	Scl	supracleithrum	上匙骨
Pmx	premaxilla	前上颌骨	Smx	supramaxilla	辅上颌骨
Pmx(r)	right premaxilla	右侧前上颌骨	Soc	supraoccipital	上枕骨
Pop	preopercular	前鳃盖骨	Soc.s	supraoccipital shelf	上枕骨嵴架
Pt	posttemporal	后颞骨	Sop	subopercular	下鳃盖骨
Pto	pterotic	翼耳骨	Sy	symplectic	续骨
PU	preural centra	尾前椎	U	ural centra	末端尾椎
Q	quadrate	方骨	UN	uroneural	尾神经骨
Sc	sclerotic ring	巩膜环			

图版说明(Explanations of plates)

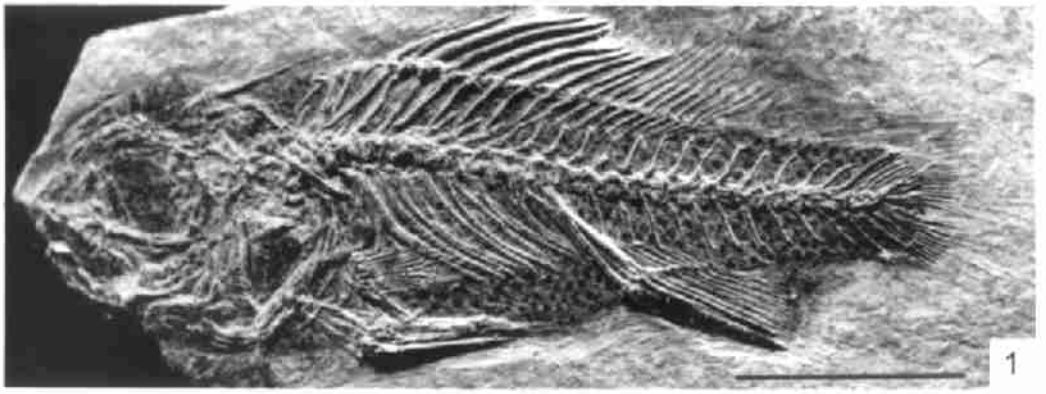
图版 I(Plate I)

1. 秀丽洞庭鳅(*T. gracilis*)，V11367.1，整鱼左侧视，湖南临澧三板桥(a complete fish in left view, Sanbanqiao, Linli, Hunan) × 3
2. 秀丽洞庭鳅(*T. gracilis*)，V11367，整鱼左侧视，湖南临澧三板桥 (a complete fish in left view, Sanbanqiao, Linli, Hunan) × 1.5
3. 下湾铺洞庭鳅(*T. hsiawanpuensis*)，V5603，整鱼右侧视，衡南龙湾滩采石场 (a complete fish in right view, Longwantan, Hengnan, Hunan) × 2
4. 秀丽洞庭鳅(*T. gracilis*)，V11367.8，尾鳍右侧视，湖南临澧三板桥 (caudal fin in right view, Sanbanqiao, Linli, Hunan) × 4
5. 秀丽洞庭鳅(*T. gracilis*)，V11367.14，鱼体前部右侧视，湖南临澧三板桥 (anterior part of a complete fish in right view, Sanbanqiao, Linli, Hunan) × 3

图版 II(Plate II)

1. 具较大锯齿之泪骨 lachrymal with gross serration
2. 秀丽洞庭鳅(*T. gracilis*)，V11367.8，尾骨骼右侧视(caudal skeleton in right view)
3. 秀丽洞庭鳅(*T. gracilis*)，V11367.10，尾骨骼右侧视(caudal skeleton in right view)
4. 下湾铺洞庭鳅(*T. hsiawanpuensis*)，V5603，尾骨骼左侧视(caudal skeleton in left view)
5. 秀丽洞庭鳅(*T. gracilis*)，V11367.10，鳃盖系统左侧视(opercular series in left view)
6. 秀丽洞庭鳅(*T. gracilis*)，V11367，鳞片上较短的栉(scales with short ctenii)
7. 下湾铺洞庭鳅(*T. hsiawanpuensis*)，V5603，鳞片上较长的栉(scales with long ctenii)
8. 下湾铺洞庭鳅(*T. hsiawanpuensis*)，V1105.1，鳞片上较长的栉(scales with long ctenii)

Scale bar in Fig.5 = 5mm, in the rest figures = 2mm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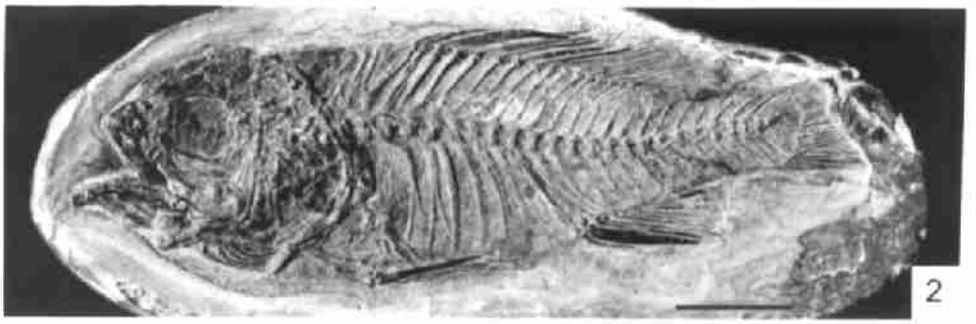
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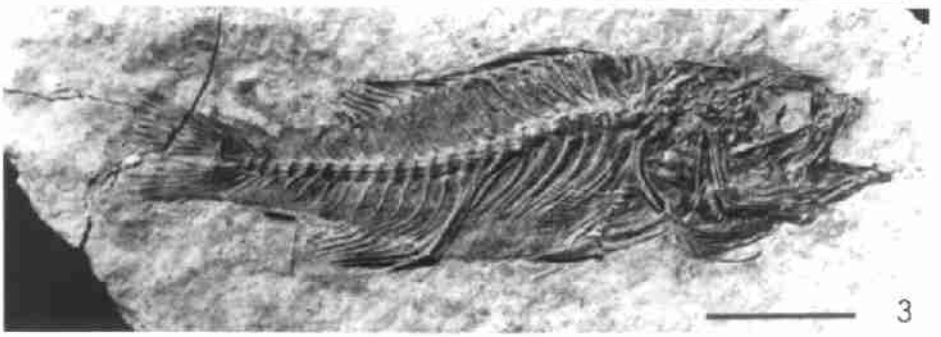
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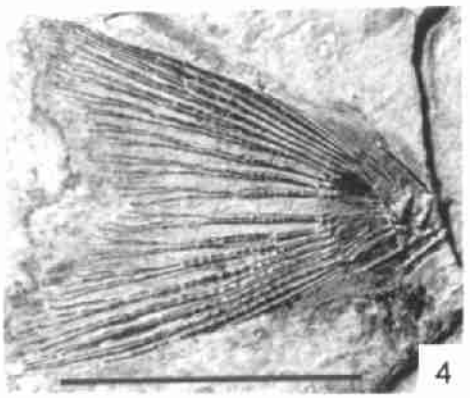
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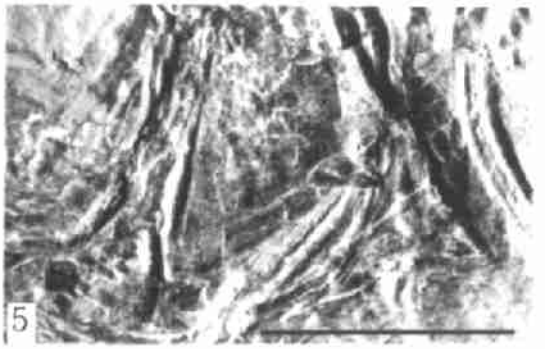
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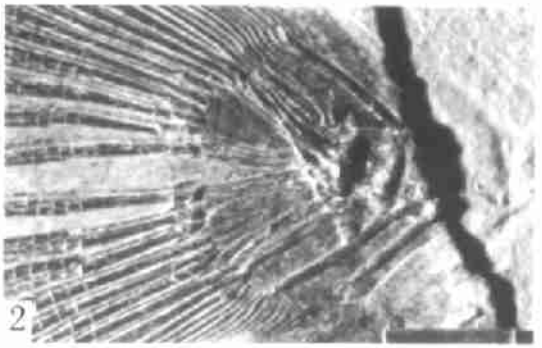
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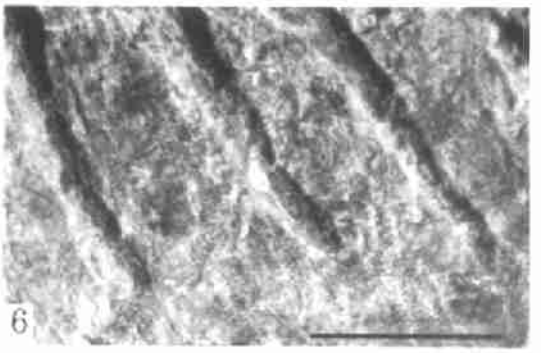
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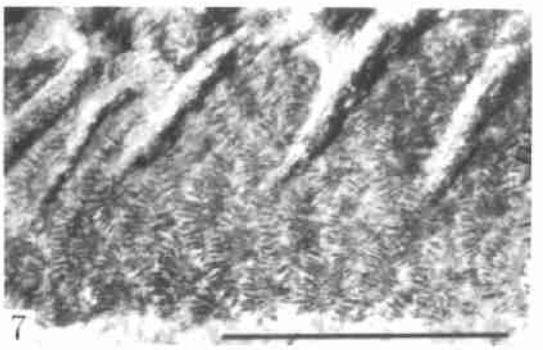
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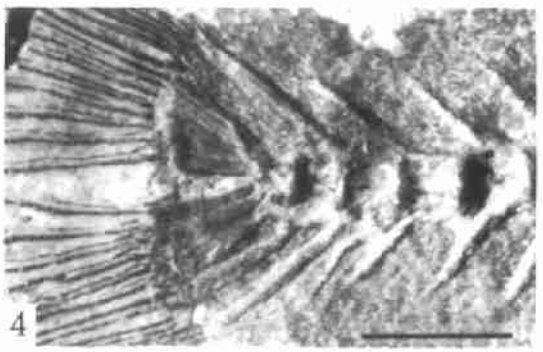
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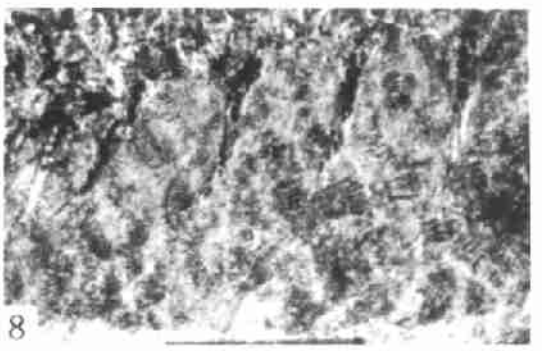
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