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## 真骨鱼类肌间刺的发育与进化

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**摘要:** 肌间刺是真骨鱼类特有性状之一,也是中国淡水养殖鱼类深加工的一个主要障碍,目前已培育出一些无肌间刺的鲤科鱼类,对于淡水养殖鱼类深加工有重要意义。肌间刺发育关键基因已逐渐明确,但对于真骨鱼类肌间刺发育的调控机制和进化机制的理解仍不清晰。针对肌间刺的类型、肌间刺在真骨鱼类的分布、肌间刺在鱼类游泳中的作用、不同游泳方式鱼类肌间刺的产生模式、肌间刺发育的细胞学基础、肌间刺发育的分子调控机制、真骨鱼类肌间刺的进化机制等方面研究进展进行了系统综述,提出了针对真骨鱼类肌间刺发育和进化的初步解析,希望进一步推动真骨鱼类肌间刺的深入研究。

**关键词:** 肌间隔; 肌间刺; 发育; 进化; 真骨鱼类

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大多数鱼类的游泳依赖大侧肌的肌纤维收缩,大侧肌由肌间隔(Myosepta)分开的许多肌节组成,大侧肌各肌节的收缩,导致躯体和尾鳍的摆动。鱼类肌间隔存在肌腱样结缔组织(Myoseptal tendon),或硬骨化的肌间刺(Intermuscular bone,也称肌间骨)。十几年来,国内外众多水产养殖学高校和研究所重视无肌间刺鲤科鱼类的育种工作,希望能培育出无肌间刺的经济鲤科鱼类,由此兴起了对鱼类肌间刺的研究<sup>[1-12]</sup>。已有文献报道,通过基因编辑培育出无肌间刺的鲤科鱼类,也有一些关于肌间刺研究的综述,介绍了肌间刺研究的进展<sup>[13-15]</sup>。尽管如此,关于对真骨鱼类肌间刺发育的调控机制及进化规律的理解尚不够明晰。本研究试图从肌间刺发育调控及进化的角度,通过梳理文献,以更好地理解真骨鱼类肌间刺的发生。

### 1 肌间刺的类型

1845年MÜLLER首先提出真骨鱼类这个类群时,就把肌间刺作为真骨鱼类的一个主要特征<sup>[16]</sup>。真骨鱼类的肌间刺是由肌间隔的肌腱骨化而成的,鱼类肌间隔有垂直肌间隔和水平肌间

隔,每个垂直肌间隔有6个肌腱:1个髓弓肌腱(Epineural tendon, ENT),1个轴上侧向肌腱(Epaxial lateral tendon, eLT),1个脉弓肌腱(Epileural tendon, EPT),1个轴下侧向肌腱(Hypaxial lateral tendon, hLT)和2个锥状肌腱(Myorhabdoid tendons, MT)(图版I-1)。真骨鱼类垂直肌间隔的肌腱部分会骨化成为肌间刺,髓弓小骨(Epineural bone)是由髓弓肌腱ENT和轴上侧向肌腱eLT共同骨化而成的(图版I-3),直接或间接连接在脊椎髓弓上<sup>[17]</sup>。脉弓小骨(Epileural bone)是由脉弓肌腱EPT和轴下侧向肌腱hLT骨化而成(图版I-4),附在腹肋或脊椎脉弓上<sup>[17]</sup>。背腹两侧的锥状肌间小骨(Myorhabdoid bone)由锥状肌腱MT骨化而成(图版I-3,图版I-4)<sup>[18]</sup>。不同真骨鱼类的髓弓小骨形态,有I形、卜形、Y形、一端多叉形、两端两分叉形、两端多叉形和树枝形等7种类型,而脉弓小骨有树枝形之外的其他6种形态<sup>[19]</sup>。除了I形仅由侧向肌腱(eLT或hLT)骨化而成以外,其他几种形态都由髓弓肌腱ENT或脉弓肌腱EPT不同程度的参与骨化而成。而位于背腹两侧的锥状肌间小骨,只出现在高体小鳀(Anchoa

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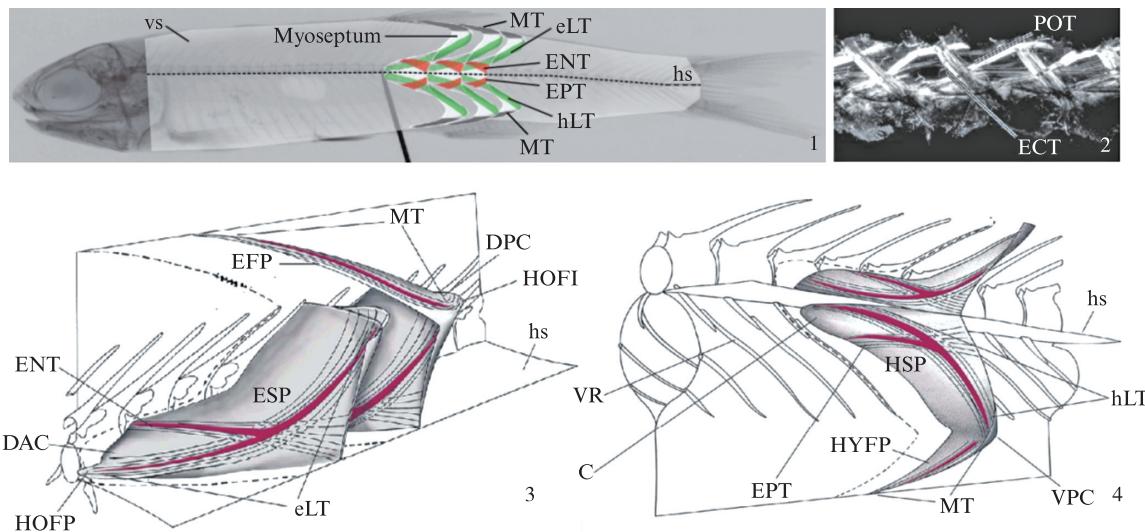
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*compressa*)、刀鲚(*Coilia nasus*)、裸背电鳗目的*Sternorhynchus*属等少数真骨鱼类类群<sup>[20-22]</sup>。鱼类水平肌间隔(Horizontal septa)由后外侧的胶原纤维(Posterolateral collagen fibres)和前外侧的胶原纤维(Anterolateral collagen fibres)交织形成,前侧的肌腱(Anteriorly oriented tendon, AOT)或称椎体肌腱(Epicentral tendon, ECT)以及后侧的肌腱(Posteriorly oriented tendon, POT)(图版 I - 2),都

有可能骨化为椎体小骨(Epicentral bone),连到椎体上<sup>[17]</sup>,椎体小骨形态比较简单,只有I形、Y形和一端多叉3种类型<sup>[23]</sup>。

国内关于鱼类肌间刺形态的报道,最早在鲫(*Carassius auratus*)骨骼的研究中涉及到<sup>[24]</sup>,此后在鲤(*Hypophthalmichthys molitrix*)系统解剖研究中有肌间刺形态和数目的描述<sup>[25]</sup>,后来又调查了几种常见鲤科(Cyprinidae)鱼类肌间刺形态<sup>[26]</sup>。



1. 真骨鱼类垂直肌间隔的肌腱类型;2. 偏振光显微镜下水平肌间隔的2组肌腱(ECT, POT);3. 轴上肌示意图:3组肌腱(ENT, eLT, MT),红色表示部分肌腱骨化成为肌间刺;4. 轴下肌示意图:3组肌腱(EPT, hLT, MT),红色表示部分肌腱骨化成为肌间刺;ENT. 髓弓肌腱;EPT. 脉弓肌腱;hLT. 轴下侧向肌腱;eLT. 轴上侧向肌腱;MT. 锥状肌腱;DPC. 背面后肌肉圆锥;HOFP. 水平扇状突出部分;vs. 垂直肌间隔;hs. 水平肌间隔;ESP. 轴上倾斜部分;EFP. 轴上侧翼部分;DAC. 背面前肌肉圆锥;VR. 腹肋;VPC. 腹面后肌肉圆锥;VAC. 腹面前肌肉圆锥;HSP. 轴下倾斜部分;HYFP. 轴下侧翼部分;POT. 后侧肌腱;ECT. 椎体肌腱。

1. Collagen-fibre architecture of vertical myosepta in teleostomes; 2. Polarized-light micrographs of horizontal septa. 3. Schematic representations of Epaxial part, oblique dorsal and anterior view. A set of three tendons (ENT, eLT, MT) is present. Red indicates possible membranous ossifications of these tendons. 4. Schematic representations of Hypaxial part, oblique ventral and anterior view. A set of three tendons (EPT, hLT, MT) is present. Red indicates possible membranous ossifications of these tendons; ENT. epineurial tendons; EPT. epipleural tendons; hLT. hypaxial lateral tendon; eLT. epaxial lateral tendon; MT. myorhabdoid tendons; DPC. dorsal posterior cone; HOFP. horizontal fanlike projections; vs. vertical septa; hs. horizontal septum; ESP. epaxial sloping parts; EFP. epaxial flanking part; DAC. dorsal anterior cone; VR. ventral ribs; VPC. ventral posterior cone; VAC. ventral anterior cone; HSP. hypaxial sloping parts; HYFP. hypaxial flanking part; POT. posteriorly oriented tendon; ECT. epicentral tendon.

图版 I 垂直肌间隔和水平肌间隔的肌腱类型和肌间刺类型

Plate I Spatial arrangement and collagen-fibre architecture of myoseptum

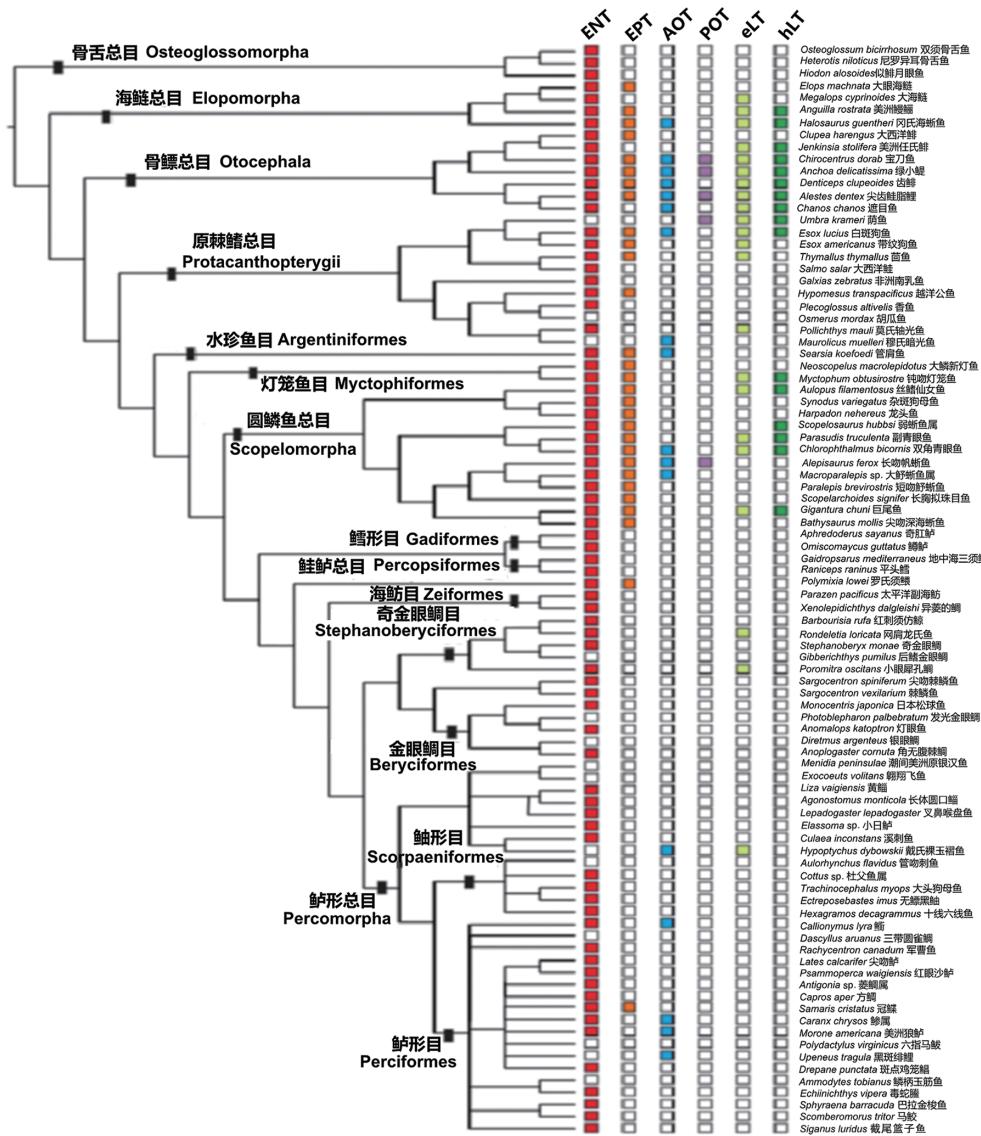
## 2 肌间刺在真骨鱼类的分布

绝大多数真骨鱼类都有肌间刺,尤其是髓弓肌腱ENT在绝大多数真骨鱼类都有不同程度的骨化,ENT、EPT、AOT、POT、eLT和hLT这6种类型肌腱都没有骨化为肌间刺的只有少数几个类群,如胡瓜鱼(*Osmerus mordax*)、后鳍金眼鲷(*Gibberichthys pumilus*)、眼灯眼鱼(*Photoblepharon palpebratum*)、黑银眼鲷(*Diretmus argenteus*)、潮间美洲原银汉鱼(*Menidia peninsulae*)、翱翔飞鱼(*Exocoetus volitans*)、

管吻刺鱼(*Aulorhynchus flavidus*)、三带圆雀鲷(*Dascyllus aruanus*)、童多指马鲅(*Polydactylus virginicus*)、玉筋鱼(*Ammodytes tobianus*)等(图1)。EPT、eLT、hLT和POT在绝大多数低等真骨鱼类(非棘鳍鱼类)中骨化,AOT在少量低等或高等真骨鱼类中骨化(图1)<sup>[27]</sup>。AOT和POT骨化而成的椎体小骨,存在于驼背鱼属(*Notopterus*)、大海鲢属(*Megalops*)、鲱形目(Clupeiforms)、鼠𬶮目(Gonorynchiforms)、裸背电鳗亚目(Gymnotoids)、茴鱼属(*Thymallus*)、仙女鱼目(Aulopiforms)的副青眼鱼属(*Parasudis*)、帆

蜥鱼属(*Alepisaurus*)和锤颌鱼属(*Omosudis*)，而在副棘鳍总目(Paracanthopterygians)、奇金眼鲷目

(Stephanoberyciforms)和鲈形目(Percomorphs)一些种类不存在椎体小骨<sup>[17,23]</sup>。



ENT. 垂直肌间隔的髓弓肌腱; EPT. 垂直肌间隔的脉弓肌腱; AOT. 水平肌间隔的前侧肌腱; POT. 水平肌间隔的后侧肌腱; eLT. 垂直肌间隔的轴上侧向肌腱; hLT. 垂直肌间隔的轴下侧向肌腱。

ENT. epineurial tendon; EPT. epipleural tendon; AOT. anteriorly oriented tendon; POT. posteriorly oriented tendon; eLT. epaxial lateral tendon; hLT. hypaxial lateral tendon.

图1 真骨鱼类水平肌间刺的分布情况(88个代表种)

Fig. 1 Distribution of tendon ossification on a supertree from family-level phylogenies ( $n=88$  taxa)

在低等真骨鱼类, 肌间刺形态和分布呈现一定的系统发育相关性<sup>[19,23]</sup>。髓弓小骨从最原始的真骨鱼类骨舌鱼总目开始出现, 其仅分布在躯干前部肌间隔, 形态均为最简单的“I”形; 到海鲢总目, 如日本鳗鲡(*Anguilla japonica*)肌间隔几乎都分布; 到鲱形总目, 如刀鲚(*Coilia nasus*)髓弓小骨形态变得复杂; 到骨鳔总目的鲤形目, 如鲤鳔弓小骨形态复杂性达到高峰; 从鲤形目的鳅科,

如泥鳅(*Misgurnus anguillicaudatus*)开始, 髓弓小骨明显退化, 数量明显变少, 形态也为简单的“I”形; 此后到骨鳔总目的鮟形目, 如黄颡鱼(*Pelteobagrus fulvidraco*), 髓弓小骨消失。脉弓小骨相对髓弓小骨要晚出现, 从海鲢总目, 如海鳗(*Muraenesox cinereus*)才开始出现, 随着进化, 形态也变得复杂, 但没有髓弓小骨的形态复杂; 到唇鱥(*Hemibarbus labeo*)开始出现退化, 到鮟形目

还保留形态简单的脉弓小骨<sup>[19]</sup>。椎体小骨也是从海鲢总目开始出现,海鳗和日本鳗鲡的椎体小骨的数目较多,鲱形目的美洲西鲱(*Alosa sapidissima*)和刀鲚数目变少了,形态也简单了,到骨鳔总目,如胭脂鱼(*Myxocyprinus asiaticus*)就退化了<sup>[23]</sup>。

### 3 肌间刺在鱼类游泳中的作用

鱼类肌间隔膜或肌间刺的功能被认为与肌节之间的力传输有关<sup>[28-30]</sup>。采用主轴波动方式游泳的鱼类,其动力大小跟身体弯曲的刚度有关,刚度越大,推力越大<sup>[31]</sup>。鱼类肌肉系统的张力类似于同质性横梁<sup>[32]</sup>。鱼类肌肉各向异性的张力和压力需要结合被动的和主动的机械特性来衡量。被动的机械特性主要由肌间隔<sup>[33]</sup>、皮肤和脊椎决定<sup>[31]</sup>,理论模拟研究关注肌间隔肌腱在肌肉节段之间力的传递、鱼体硬度总体上的增加和大侧肌收缩过程肌节变形程度的降低等三方面的作用<sup>[29,31,34-35]</sup>。相比肌间隔膜,肌间刺更能增加鱼体抗弯刚度,可在肌肉收缩过程阻止肌节变形,从而在鱼体摆动时帮助产生更有效的推力<sup>[31,34-37]</sup>。研究<sup>[38]</sup>表明,蓝鳃太阳鱼(*Lepomis macrochirus*)肌间隔贡献了鱼体被动抗弯刚度的一半,使鱼体如一个横梁式摆动。

为了研究肌间刺结构及对功能的影响,RHO等<sup>[39]</sup>调查了大西洋鲱(*Clupea harengus*)肌间刺从早期骨化区域到后期完全骨化区域的压痕模量,BURGER等<sup>[40]</sup>利用新式小角度X射线扫描仪分析了3~5龄的大西洋鲱和4~5龄的美洲西鲱肌间刺中的胶原纤维的超级结构,FIEDLER等<sup>[41]</sup>调查了大西洋鲱肌间刺的结构、微结构、矿物质相关的性能以及微机械力的拉伸特征等,得出大西洋鲱肌间刺有很好的抗变形能力。研究发现侧向肌腱LTs及其骨化的肌间刺,主要与力的传送有关,而ENT和EPT及其骨化的肌间刺主要与内部压力产生有关<sup>[33]</sup>。

### 4 不同游泳方式鱼类肌间刺的形成模式

鱼类游泳方式分为MPF(Median or paired-fin swimming)方式和BCF(Body-caudal fin swimming)方式,MPF方式仅依靠鳍的摆动或拍打产生推力,如鲀科鱼类,很少有肌间刺。BCF方式是大多数鱼类的游泳方式,有鳗行式、亚鲹

行式、鲹行式和鲔行式,肌间刺主要存在于鳗行式、亚鲹行式和鲹行式这3种游泳方式的真骨鱼类中<sup>[17,42]</sup>。

真骨鱼类孵化后,肌间隔先出现肌腱样结缔组织膜,经过一段时间后才可能逐步形成肌间刺。国内最早在鲤中观察到肌间刺的发育过程<sup>[37]</sup>,国外在一些种类中也有简单描述<sup>[17,42]</sup>,亚鲹行式或鲹行式鱼类中,如斑马鱼(*Danio rerio*)、鲢、欧江彩鲤(*Cyprinus carpio* var. *Color*)、唇锯、黄河鲤(*Cyprinus carpio haematopterus*)、鲫、团头鲂(*Megalobrama amblycephala*)等的肌间刺形成顺序都是先出现在尾部,然后往前依次出现<sup>[43-49]</sup>,例如,鲢肌间刺在受精后43 d(dpf)首先在尾部肌间隔形成,然后往头部方向依次形成,到55 dpf在各肌间隔基本全部形成。不同于亚鲹行式或鲹行式鱼类依赖身体后部的强力摆动来完成游泳,鳗行式鱼类则依赖于整个身体从前到后扭动<sup>[50-52]</sup>,鳗行式游泳的日本鳗鲡,其肌间刺形成顺序则是从躯干部前部肌间隔逐渐到尾部,与亚鲹行式或鲹行式游泳的鱼类相反<sup>[53-54]</sup>,在同样属于鳗行式的黄鳝和泥鳅中,肌间刺形成顺序也是如此<sup>[55]</sup>。这种不同游泳方式鱼类肌间刺形成顺序的不同,提示鱼体摆动时肌肉传递过来的机械力可能诱导了肌间刺的形成<sup>[56]</sup>。

### 5 肌间刺发育的细胞学基础

肌间刺是膜性硬骨,由间充质细胞分化为成骨细胞,而不经过软骨阶段<sup>[18,27,43]</sup>。也有少量报道,发现在一些鱼类先成为软骨,再骨化为硬骨<sup>[27]</sup>。在斑马鱼和虹鳟(*Oncorhynchus mykiss*)胚胎2体节阶段,发现体节区域生骨节的间充质细胞迁入肌间隔<sup>[57-58]</sup>,斑马鱼肌间隔存在*scxa*基因表达的间充质细胞,既可分化为肌腱细胞(Tenocyte),表达肌腱细胞标记基因(*tnmd*、*colla2*、*xir2b*),又可分化为成骨细胞(Osteoblast),表达成骨细胞标记基因(*runx2b*)<sup>[59]</sup>。敲除斑马鱼*scxa*基因,可导致肌间骨缺失<sup>[59-60]</sup>,表明鱼类的肌间刺是表达*scxa*基因的间充质细胞分化的结果。敲除肌腱细胞标记基因*tnmd*、*colla2*或*xir2b*,是否有可能影响肌间刺形成?如果不影响,表明肌间刺的成骨细胞是直接由间充质细胞分化而成。

## 6 肌间刺发育的分子调控机制

肌间刺是在鱼类胚后阶段形成的,而且不同游泳方式鱼类肌间刺形成模式不同,表明肌间隔间充质细胞受到了鱼体摆动或扭动的挤压,因此,肌间刺形成可能是机械力诱导的结果(图2)。已知来源于人脊髓的间充质细胞在机械力刺激下,可分化为硬骨、软骨、脂肪、皮肤、肌腱、肌肉等组织<sup>[61-65]</sup>。Myostatin (MSTN)是调控骨骼肌发育的关键基因,Follistatin (FST)有拮抗MSTN的作用<sup>[66]</sup>,*mstn*<sup>-/-</sup>斑马鱼肌肉松弛,肌间刺明显变大,而且肌间刺出现的时间提前,相反*fst*<sup>-/-</sup>斑马鱼肌肉紧密,肌间刺明显变短,而肌间刺出现的时间延迟<sup>[67]</sup>。

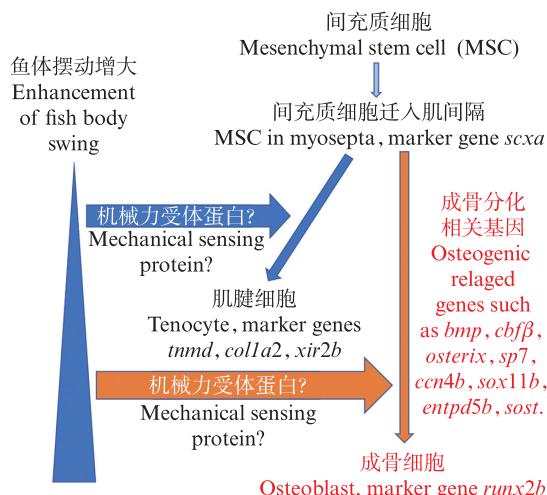


图2 真骨鱼类肌间刺发育的分子调控机制  
Fig. 2 Molecular regulation of intermuscular bones development in teleosts

已知机械感受通道蛋白 Piezo1 是调节血管张缩和骨骼内部动态平衡的机械力受体蛋白<sup>[68-69]</sup>,而另一个机械感受通道蛋白 Piezo2 负责呼吸道组织感受呼吸运动往复扩张和压缩的机械感受<sup>[70]</sup>,可见,Piezo 离子通道可以感受不同频率的机械力刺激,很可能参与调控鱼类肌间刺的发育。另一个能感受多种机械力类型的蛋白 TRPV4 在斑马鱼肌间刺发育过程中的作用也需研究<sup>[71-72]</sup>。

间充质细胞分化为成骨细胞通过细胞信号传导通路和转录因子调控两个过程,细胞信号传

导通路相关的基因包括 *wnt*、*bmp*、*tgf-β*、*hedgehog*、*pth*、*fgf*、*ephrin*、*notch*、*hippo* 和 *piezo1/2*,促进成骨细胞分化、骨形成和稳定,与成骨细胞分化相关的主要转录因子有 *runx2*、*cbfβ*、*runx1*、*osterix*、*atf4*、*satb2* 和 *taz/yap*<sup>[73]</sup>,这些基因都有可能参与肌间刺发育的调控<sup>[15]</sup>。利用 Crispr/Cas9 技术敲除 *bmp6*,可以得到无肌间刺的斑马鱼和鲫<sup>[74-75]</sup>,或减少翘嘴鲌(*Culter alburnus*)的肌间刺数目<sup>[76]</sup>,*bmp6* 敲除对鲢肋骨形成有一定的影响<sup>[77]</sup>。敲除 *runx2b* 基因,可以得到无肌间刺的斑马鱼、团头鲂、银鲫(*Carassius gibelio*)<sup>[78-80]</sup>,对其他骨骼和肌肉都没有明显的影响。此外,敲除 *sp7*、*taz*、*msxC* 等基因也会影响肌间刺的发育<sup>[81-84]</sup>。

除了功能验证的与肌间刺发育相关基因,一些鱼类肌间刺转录组、基因组和蛋白组等组学也提供了一些相关基因信息<sup>[78,85-90]</sup>,可采用原位杂交等显示有些基因在肌间隔表达<sup>[91-92]</sup>,这些基因有待今后进一步功能验证。

## 7 真骨鱼类肌间刺进化的可能机制

不同真骨鱼类都有自己独特的生态位,对游泳能力的要求也不一样。对于游泳能力有一定要求的鱼类,如果大侧肌强度不够,其需要增加鱼体摆动频率,来满足游泳的要求,这样就有更多挤压肌间隔的机会,肌间隔的间充质细胞就有可能分化出更多的成骨细胞,形成更强壮的肌间刺;如果大侧肌强度足够,鱼体每次摆动,能达到足够的推力,鱼体的摆动频率就低,较低的鱼体摆动频率,可能不足以刺激间充质细胞分化为成骨细胞,只能形成肌腱细胞,这样导致肌间骨不容易形成。而对于游泳能力没有要求的鱼类,如埋栖型鱼类,不管大侧肌强还是弱,鱼体摆动频率太低,难以刺激肌间隔的间充质细胞分化为成骨细胞,更难以形成肌间刺(图3)。因此,决定一种鱼类是否会形成肌间刺,首先与鱼的游泳能力要求高低有关,其次与大侧肌强度有关。YANG 等<sup>[93]</sup>也发现尽管鲤科鱼类的肌间刺表型呈现一定的系统关系,但肌间刺形成和形态复杂性更多与生态因子如摄食类型有关。

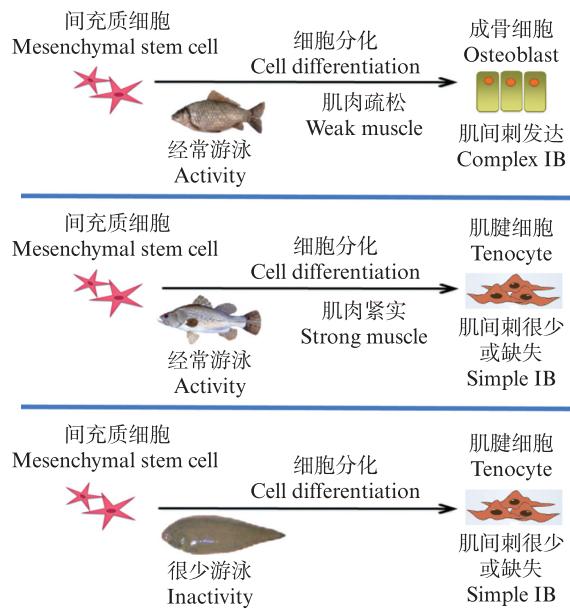


图3 真骨鱼类肌间刺多样性进化的解释

Fig. 3 Scheme explanation on the evolution of intermuscular bones in teleosts

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## The development and evolution of intermuscular bones in teleosts

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**Abstract:** Intermuscular bone (IB) is one of three morphological characters of teleosts, and is becoming an obstacle for fish processing. Recently, some cyprinid fish without IB have been generated by Crispr/Cas9 technology, will be very helpful for our fresh fish culture in China. So far *bmp6* and *runx2b* have been determined as key genes for the development of IBs, however, upstream signal pathway to regulate the development is not sure, and the complex evolution of IBs in teleost is in lack of understanding. This review first gives us a basic introduction on the IB types, distribution, and the role in swimming, then focuses on the research advance on IB developmental model, cellular origin, and upstream regulation factors. Finally, a preliminary hypothesis is proposed in this review to explain IB evolution in teleosts, indicating IB evolution potential associations between axial muscle diversification and locomotion adaptive radiations that generated modern teleost lineages.

**Key words:** myosepta; intermuscular bone; development; evolution; teleost