COMPARATIVE OSTEOLOGY OF THE FISHES OF THE FAMILY LEIOGNATHIDAE

PART II: RELATIONSHIPS AMONG THE GENERA AND THE SPECIES*

P. S. B. R. JAMES
Central Marine Fisheries Research Institute, Cochin 682018.

While the three genera, *Leiognathus, Secutor* and *Gazza,* in the family Leiognathidae share some osteological characters in common, they differ from one another strikingly in certain characters (Table 2). The differences between the genera appear to be more pronounced in the otic region of the skull than elsewhere.

The differences between *Leiognathus* and *Secutor,* between *Leiognathus* and *Gazza* and between *Secutor* and *Gazza* are shown in Tables 3 to 5 respectively. The study indicates that osteologically the genus *Leiognathus* is more distantly related to *Secutor* than *Leiognathus* to *Gazza* or *Secutor* to *Gazza.*

Details of 23 salient osteological characters of the species of *Leiognathus, Secutor* and *Gazza* are summarised in Table 6. As may be seen from the Table, while some species possess one or more characters distinguishing from others, some other species share certain characters with a few others which distinguish them from the remaining species. Sixteen such characters are denoted accordingly in Table 7 to indicate the divergence and convergence between species.

Divergence

The distinguishing characters of the species are listed below:

L. fasciatus: the epiotic process is club-shaped.

L. equulus: the sphenotics are broad, nuchal spine is largest, epiotic process is narrow and sharp.

L. smithursti: hyomandibular with two prominent processes along the front margin; last branchiostegal ray arises from the epihyal.

L. splendens: premaxillary shows forward inclination.

---

* For sections such as Introduction, Material and Methods, common also to this part, Part II, *see* Part I; OSTEOLOGY, published in Number 3 of this volume.

L. jonesi: epiotic process comparatively small, posterior process of basisphenoid conspicuously long.

L. dussumieri: posterior process of palatine very long.

L. daura: parasphenoid has a bulbous projection below dorsal process; quadrate has a process at upper posterior corner.

L. blochi: posterior part of vomer very short, entopterygoid has a bifid process.

L. brevirostris: occipital crest is very small, lower arm of preopercle curved.

L. leuciscus: no distinguishing character found.

L. berbis: no distinguishing character found.

L. lineolatus: anterior margin of basioccipital conspicuously denticulated.

L. bindus: no distinguishing character found.

S. ruconius: occipital crest 90° to front margin of eye.

S. insidiator: inner process of premaxillary very narrow.

G. minuta: no distinguishing character found.

G. achlamys: orbital cavity conspicuously large.

Convergence

Table 7 indicates a close relationship between *L. smithursti* and *L. splendens* in characters like the conspicuous bifid posterior end of parasphenoid, blunt and stumpy epiotic process, conspicuously short posterior process of basisphenoid and bent upper and lower arms of maxillary. However, *L. smithursti* appears to be less closely related to *L. jonesi* than to *L. splendens* in the deeply forked anterior end of vomer, maxillary having bent upper and lower arms and in the prominent process at upper posterior corner of the opercle. Although there is close external similarity between *L. splendens* and *L. jonesi* osteologically, they do not exhibit similarity in characters except in the bent upper and lower arms of the maxillary which is a common character for many other species also. *L. jonesi* appears to be closely related to *L. smithursti* than to *L. splendens*. Thus, the three species are akin to each other and widely separated from others.

Apart from the common characters *viz.*, bent upper and lower arms of the maxillary *L. dussumieri* shares with *L. smithursti, L. splendens* and *L. jonesi, L. dussumieri* appears closely related to *L. smithursti* and *L. splendens* in the conspicuous bifid posterior end of parasphenoid and the blunt and stumpy epiotic process.

Similarly, *L. fasciatus* and *L. equulus* are closely related to each other, than to other species. These two species share the common characters of conspicuous bony lemella of the parasphenoid, large inner process of the premaxillary, bent upper and lower arms of maxillary and the conspicuous lower process of the entopterygoid.

TABLE 1. *Distinguishing osteological characters of* Leiognathus, Secutor *and* Gazza.

Character	*Leiognathus*	*Secutor*	*Gazza*
I. *Orbital region*			
1. Lacrymal	Antero-ventral portion short and blunt	Antero-ventral portion short and somewhat sharp	Antero-ventral portion long and sharp
II. *Otic region*			
2. Parietals	Rectangular, with strong ridges dorsally	Oblong with narrow ridges dorsally	Ovoid, with delicate ridges dorsally
3. Supraoccipital crest	Upper half of posterior margin of crest crenulated, lower half concave	Upper half of posterior margin of crest smooth lower half concave	Entire posterior margin wavy
4. Sphenotic	Narrow and long, cavity not partitioned	Narrow and long, cavity partitioned	Broad and short cavity partitioned
5. Exoccipital	Paraoccipital condyles small and flat	Paraoccipital condyles large and concave	Paraoccipital condyles large and flat
III. *Basicranial region*			
6. Parasphenoid	Middle portion bears a broad fringe of bone on the ventral side	Fringe absent	Fringe narrow
7. Basisphenoid	Ventral portion prominent	Dorsal and ventral portions smallest	Dorsal portion largest, ventral smaller than in *Leiognathus* but larger than in *Secutor*
8. Basciocciptal	Dorsal cavities shallow	No dorsal cavities	Dorsal cavities deep
IV. *Oromandibular region*			
9. Metapterygoid	Anterior and posterior fringes present	Fringes absent	Only a small anterior fringe present
10. Hyomandibular	Anterior fringe broader, both fringes terminating ventrally at the same point	Both fringes least developed, posterior ending below anterior	Posterior fringe best developed, ending below anterior

TABLE 2. *Differences between* Leiognathus *and* Secutor.

Character	*Leiognathus*	*Secutor*
I. *Olfactory region*		
1. Dermethmoid	No posterior horizontal limb	Posterior horizontal limb present
2. Prefrontals	With an oblique ridge dorsally	No ridge
3. Nasals	Anterior part broad and blunt	Anterior part narrow and sharp
4. Vomer	Posterior portion short and stout	Posterior portion long and narrow
II. *Orbital region*		
5. Frontals	Narrow with thick rounded bony edges	Broad with sharp elevated ridges
6. Alisphenoids	Rectangular, inner ridge absent	Oval, inner ridges less prominent
7. Lacrymal	Anteroventral portion blunt	Anteroventral portion sharp
III. *Otic region*		
8. Parietals	Rectangular with strong bony ridges	Oblong with narrow dorsal ridges
9. Supraoccipital	Convex No bend in supraoccipital spine High crest, upper half of posterior margin of crest crenulated	Less convex Bend in supraoccipital spine Low crest, upper half of posterior margin of crest smooth
10. Pterotic	Bears a large cavity	Bears a small cavity
11. Epiotic	Less convex, the process short	More convex, the process long
12. Sphenotic	Narrow and long, cavity not partitioned	Narrow and long, cavity partitioned
13. Exoccipital	Paraoccipital condyles small and flat	Paraoccipital condyles large and concave
IV. *Basicranial region*		
14. Parasphenoid	Anterior end broad Middle portion (about 1/3 length) bears a broad fringe of bone on ventral side	Anterior end narrow Fringe absent
15. Basisphenoid	Ventral portion prominent	Ventral portion not prominent
16. Basioccipital	Dorsal cavities shallow	No dorsal cavities

TABLE 2. (*contd.*)

Characters	*Leiognathus*	*Secutor*
V. *Oromandibular region*		
17. Premaxilla	Vertical limb curved Horizontal limb makes an angle of less than 90° with vertical limb Outer and inner process from horizontal limb small	Vertical limb straight Horizontal limb makes an angle of 90° with vertical limb Outer and inner processes from horizontal limb conspicuously large
18. Maxilla	Short and broad	Long and narrow
19. Dentary	Triangular in shape	L-shaped
20. Metapterygoid	Anterior and posterior fringes present	Fringes absent
	No notches on anterior and posterior margins	Notches present in anterior and posterior margins
	Base of metapterygoid occupies the entire dorsal margin of quadrate	Base of metapterygoid occupies the posterior 3/4 of dorsal margin of quadrate
21. Ectopterygoid	Sharp at both ends	Broad and blunt at anterior end, narrow and sharp at posterior end
	Anterior half of bone bears a prominent ridge	No ridge
22. Entopterygoid	Oblong	Somewhat triangular
23. Quadrate	Quadrate and metapterygoid united by bony fibrous connections	No bony fibrous connections between quadrate and metapterygoid
24. Preopercle	Fringe of bone at inner angle absent	Fringe of bone at inner angle present
25. Hyomandibular	Anterior fringe broader, both fringes terminating at the same point ventrally	Both fringes least developed posterior ending below anterior

Although the three species, viz., *L. leuciscus, L. berbis* and *L. lineolatus*, resemble one another externally, the osteological characters indicate that *L. berbis* and *L. lineolatus* are closer to each other than *L. leuciscus* to either of them. The characters shared by the three species include the conspicuous bifid posterior end of parasphenoid, blunt and stumpy epiotic process, bent upper and lower arms of the maxillary and the sharp tip of the upper arm of the maxillary.

TABLE 3. *Differences between* Leiognathus *and* Gazza.

Character	*Leiognathus*	*Gazza*
I. *Olfactory region*		
1. Vomer	Posterior portion short and stout	Posterior portion long and narrow
II. *Orbital region*		
2. Frontals	Narrow with thick rounded bony ridges	Broad with sharp elevated ridges
3. Circumorbital series	Represented by dermosphenotic	Represented by dermosphenotic and another bone
III. *Otic region*		
4. Supraoccipital	Convex No bend in supraoccipital spine Supraoccipital crest high, does not extend beyond the bone	Less convex Supraoccipital spine bent Supraoccipital crest low, extends posteriorly beyond the bone
5. Pterotic	Bears a large cavity, pterotic process narrow	Bears a small cavity, pterotic process broad and wing-like
6. Epiotic	Less convex, process short	More convex, process long
IV. *Basicranial region*		
8. Premaxilla	Anterior end broad, fringe on middle portion broad, wings small	Anterior end narrow, fringe on middle portion narrow, wings prominent
V. *Oromandibular region*		
8. Premaxilla	Vertical limb curved, horizontal limb makes an angle less than 90° with vertical limb Teeth inconspicuous	Vertical limb straight, horizontal limb makes an angle of 90° with vertical limb Teeth conspicuous
9. Maxilla	Short and broad, posterior extension concave	Long and narrow, posterior extension forked
10. Dentary	Teeth minute	Teeth prominent
11. Metapterygoid	Base of metapterygoid occupies the entire dorsal margin of quadrate	Base of metapterygoid occupies the posterior 3/4 of dorsal margin of quadrate
12. Ecopterygoid	Sharp at both ends, anterior half of bone bears a prominent ridge	Broad and blunt at the anterior end, narrow and sharp at posterior end, no ridge on anterior half of the bone
13. Entopterygoid	Posterior fringe of bone absent	Posterior fringe of bone present
14. Quadrate	The spiny ridge extends fully along the posterior margin, quadrate and metapterygoid united by bony fibrous connections	The spiny ridge does not extend fully along the posterior margin, quadrate and metapterygoid not united by bony fibrous connections
15. Process on subopercle	Indistinct	Distinct
16. Preopercle	Fringe of bone at inner angle absent	Fringe of bone at inner angle present

TABLE 4. *Difference between* Secutor *and* Gazza.

Character	*Secutor*	*Gazza*
I. *Olfactory region*		
1. Dermethmoid	Posterior horizontal limb present	Posterior horizontal limb absent
2. Prefrontals	No ridges on dorsal side	Oblique ridges on the dorsal side
3. Nasals	Anterior part narrow and sharp	Aterior part broad and blunt
II. *Orbital region*		
4. Alisphenoids	Oval, inner ridge not prominent	Rectangular, inner ridge prominent
5. Circumorbital series	Represented by dermosphenotic	Represented by dermosphenotic and another bone
III. *Otic region*		
6. Supraoccipital	Crest does not extend beyond the bone	Crest extends posteriorly beyond the bone
7. Pterotic	Process narrow	Process broad and wing-like
IV. *Basicranial region*		
8. Parasphenoid	Middle portion bears on fringe, anterior 2/3 length of bone strongly curved upward, lateral wings small	Middle portion bears a narrow fringe, anterior 2/3 length of bone almost straight, lateral wings prominent
V. *Oromandibular region*		
9. Premaxilla	Outer and inner processes from horizontal limb large, teeth inconspicuous	Outer and inner processes from horizontal limb small, teeth conspicuous
10. Maxilla	Posterior extension concave	Posterior extension forked
11. Dentary	L-shaped, teeth minute	Triangular, teeth prominent
12. Metapterygoid	Fringes absent, anterior and posterior margins of metapterygoid with notches	Only a small anterior fringe present, anterior and posterior margins of metapterygoid without notches
13. Entopterygoid	Somewhat triangular no posterior fringe of bone	Oblong, posterior fringe of bone present
14. Quadrate	The spiny ridge extends fully along the posterior margin	The spiny ridge does not extend fully along the posterior margin
15. Process on subopercle	Indistinct	Distinct

TABLE 5. *Salient osteological characters of species of* Leiognathus, Secutor *and* Gazza *indicating diagnostic characters (denoted by asterisks) and characters of convergence among species.*

Characters	*L. fasciatus*	*L. equulus*	*L. smithursti*	*L. splendens*	*L. jonesi*	*L. dussumieri*
1. Occipital crest	—	—	—	—	—	—
2. Orbital cavity	—	—	—	—	—	—
3. Vomer	—	—	anterior end deeply forked	—	anterior end deeply forked	—
4. Sphenotics	—	broad*	—	—	—	—
5. Nuchal spine	—	largest*	—	—	—	Small
6. Parasphenoid	bony lamella on ventral side conspicuous	bony lamella on ventral side conspicuous	posterior end conspicuously bifid	posterior end conspicuously bifid	—	Posterior end conspicuously bifid
	L. daura	*L. blochi*	*L. brevirostris*	*L. leuciscus*	*L. herbis*	*L. lineolatus*
1. Occipital crest	—	—	very small*	—	—	—
2. Orbital cavity	—	—	—	—	—	—
3. Vomer	—	Posterior part very short*	—	—	anterior end deeply forked	anterior end deeply forked
4. Sphenotics	—	—	—	—	—	—
5. Nuchal spine	—	—	—	—	small	small
6. Parasphenoid	bulbous projection below dorsal process;* Posterior end conspicuously bifid	—	posterior end conspicuously bifid	posterior end conspicuously bifid	posterior end conspicuously bifid	posterior end conspicuously bifid

	L. bindus	*S. ruconius*	*S. insidiator*	*G. minuta*	*G. achlayms*
1. Occipital crest	—	90° to front margin of eye*	—	—	—
2. Orbital cavity	—	—	—		Conspicuously large*
3. Vomer	—	anterior and deeply forked	—	anterior end arrow shaped	anterior end arrow shaped
4. Sphenotics	—	—	—	—	—
5. Nuchal spine	—	—	small	—	—
6. Parasphenoid	anterior end points upwards	deeply curved; anterior end points upwards	deeply curved; anterior end points upwards	—	—

	L. fasciatus	*L. equulus*	*L. smithursti*	*L. splendens*	*L. jonesi*	*L. dussumieri*
7. Frontals and nuchal spine	—	—	—	—	—	—
8. Epiotic process	club shaped*	narrow and sharp*	blunt and stumpy	blunt and stumpy	comparatively small*	blunt and stumpy
9. Basisphenoid	—	—	posterior process conspicuously short	posterior process conspicuously short	posterior process conspicuously long*	—
10. Basioccipital	—	—	—	—	—	—
11. Premaxillary	inner process large	inner process large	inner process large	forward inclination	—	—

TABLE 5 (*contd.*)

12. Maxillary	upper and lower arms bent	upper and lower arms bent	upper and lower arms bent	upper and lower arms bent; tip of upper sharp; middle process sharp	upper and lower arms bent	upper and lower arms bent
	L. daura	*L. blochi*	*L. brevirostris*	*L. leuciscus*	*L. berbis*	*L. lineolatus*
7. Frontals and nuchal spine	—	—	—	—	—	—
8. Epiotic process	blunt and stumpy	blunt and stumpy	blunt and stumpy	blunt and stumpy	blunt and stumpy	blunt and stumpy
9. Basisphenoid	posterior process conspicuously short	posterior process bent	posterior process conspicuously short	—	—	posterior process bent
10. Basioccipital	—	—	—	—	—	anterior margin conspicuously denticulated*
11. Premaxillary	teeth inconspicuous	teeth inconspicuous	inner process large	—	—	—
12. Maxillary	upper and lower arms bent; middle process sharp	upper and lower arms bent; tip of upper arm sharp	upper and lower arms bent; tip of upper arm sharp	upper and lower arms bent; tip of upper arm sharp	upper and lower arms bent; tip of upper arm sharp	upper and lower arms bent; tip of upper arm sharp
	L. bindus	*S. ruconius*	*S. insidiator*	*G. minuta*	*G. achlamys*	
7. Frontals and nuchal spine	—	—	—	form a straight line	form a straight line	

8. Epiotic process	blunt and stumpy	blunt and stumpy	blunt and stumpy	blunt and stumpy	blunt and stumpy	
9. Basisphenoid	posterior process conspicuously short	—	—	posterior process conspicuously short	inner cavity very deep*	
10. Basioccipital	—	—	—	—	—	
11. Premaxillary	—	teeth inconspicuous	inner process very narrow* teeth inconspicuous	inner process large; teeth prominent	inner process large; teeth prominent	
12. Maxillary	lower arm straight; middle process sharp	—	—	lower arm straight; middle process sharp	lower arm straight; middle process sharp	

	L. fasciatus	*L. equulus*	*L. smithursti*	*L. splendens*	*L. jonesi*	*L. dussumieri*
13. Dentary	—	—	—	—	—	—
14. Entopterygoid	lower process conspicuous	lower process conspicuous	—	—	—	—
15. Palatine	—	—	—	—	—	posterior process very long*
16. Quadrate	—	—	—	—	—	—
17. Opercle	—	—	prominent process at upper posterior corner	—	prominent process at upper posterior corner	—

TABLE 5 (*contd.*)

18. Preopercle	—	—	sharp projection on lower arm	—	—	—
	L. daura	*L. blochi*	*L. brevirostris*	*L. leuciscus*	*L. berbis*	*L. lineolatus*
13. Dentary	teeth inconspicuous	teeth inconspicuous	—	—	—	—
14. Entopterygoid	—	bifid process present*	—	—	—	—
15. Palatine	—	—	—	—	—	—
16. Quadrate	process at upper posterior corner conspicuous*	—	—	—	—	—
17. Opercle	prominent process at upper posterior corner	—	—	—	—	—
18. Preopercle	sharp projection on lower arm	—	lower arm curved*	—	—	—
	L. bindus	*S. ruconius*	*S. insidiator*	*G. minuta*	*G. achlamys*	
13. Dentary	—	—	—	teeth well developed	teeth well developed	
14. Entopterygoid	—	—	—	—	—	
15. Palatine	—	—	—	—	—	
16. Quadrate	—	—	—	—	—	
17. Opercle	—	prominent process	prominent process at	—	—	

18. Preopercle	—	at upper posterior corner	upper posterior corner	serrations on ventral margin very prominent	serrations on ventral margin very prominent	
	L. fasciatus	*L. equulus*	*L. smithursti*	*L. splendens*	*L. jonesi*	*L. dussumieri*
19. Hyomandibular	—	—	two prominent process along front margin*	—	—	—
20. Branchiostegal rays	five	five	five	four	four	four
21. Origin of branchiostegal rays	last two from epihyal	all from ceratohyal	last one from epihyal*	all from ceratohyal	all from ceceratohyal	all from ceratohyal
22. Third hypobranchial	leaf-like	leaf-like	leaf-like	leaf-like	simple	leaf-like
	L. daura	*L. blochi*	*L. brevirostris*	*L. leuciscus*	*L. berbis*	*L. lineolatus*
19. Hyomandibular	—	—	—	—	—	—
20. Branchiostegal rays	five	four	four	four	four	four
21. Origin of branchiostegal rays	all from ceratohyal	last two from epihyal	all from ceratohyal	all from ceratohyal	all from ceratohyal	all from ceratohyal
22. Third hypobranchial	leaf-like	leaf-like	leaf-like	simple	leaf-like	leaf-like
	L. bindus	*S. ruconius*	*S. insidiator*	*G. minuta*	*G. achlamys*	
19. Hyomandibular	—	lower part rod-like	lower part rod-like	—	—	
20. Branchiostegal rays	four	four	four	five	five	
21. Origin of branchiostegal rays	all from ceratohyal	all from ceratohyal	all from ceratohyal	all from ceratohyal	all from ceratohyal	
22. Third hypobranchial	simple	leaf-like	leaf-like	leaf-like	leaf-like	

TABLE 6. *Characters of convergence and divergence among species of* Leiognathus, Secutor *and* Gazza. + : Present; — : absent

Character	*L. fasciatus*	*L. equulus*	*L. smithursti*	*L. splendens*	*L. jonesi*	*L. dussumieri*
1. Vomer						
— deeply forked anterior end	—	—	+	—	+	—
2. Nuchal spine — small	—	—	—	—	—	+
3. Parasphenoid						
— conspicuous bony lamella	+	+	—	—	—	—
— conspicuous bifid posterior end	—	—	+	+	—	+
— anterior end points upwards	—	—	—	—	—	—
— deeply curved	—	—	—	—	—	—
4. Frontals and nuchal spine forming straight line	—	—	—	—	—	—
5. Epiotic process						
— blunt and stumpy	—	—	+	+	—	+
6. Basisphenoid						
— posterior process conspicuously short	—	—	+	+	—	—
— posterior process bent	—	—	—	—	—	—

	L. daura	*L. blochi*	*L. brevirostris*	*L. leuciscus*	*L. berbis*	*L. lineolatus*
1. Vomer						
— deeply forked anterior end	—	—	—	—	+	+
2. Nuchal spine — small	—	—	—	—	+	+
3. Parasphenoid						
— conspicuous bony lamella	—	—	—	—	—	—
— conspicuous bifid posterior end	+	—	+	+	+	+

— anterior end points upwards	—	—	—	—	—	—
— deeply curved	—	—	—	—	—	—
4. Frontals and nuchal spine forming straight line	—	—	—	—	—	—
5. Epiotic process						
— blunt and stumpy	+	+	+	+	+	+
6. Basisphenoid						
— posterior process conspicuously short	+	—	+	—	—	—
— posterior process bent	—	+	—	—	—	+

	L. bindus	*S. ruconius*	*S. insidiator*	*G. minuta*	*G. achlamys*
1. Vomer					
— deeply forked anterior end	—	+	—	—	—
2. Nuchal spine — small	—	—	+	—	—
3. Parasphenoid					
— conspicuous bony lamella	—	—	—	—	—
— conspicuous bifid posterior end	—	—	—	—	—
— anterior end points upwards	+	+	+	—	—
— deeply curved	—	+	+	—	—
4. Frontals and nuchal spine forming straight line	—	—	—	+	+
5. Epiotic process					
— blunt and stumpy	+	+	+	+	+
6. Basisphenoid					
— posterior process conspicuously short	+	—	—	+	—
— posterior process bent	—	—	—	—	—

	L. fasciatus	*L. equulus*	*L. smithursti*	*L. splendens*	*L. jonesi*	*L. dussumieri*
7. Premaxillary						
— inner process large	+	+	+	—	—	—
— inconspicuous teeth	—	—	—	—	—	—
— prominent teeth	—	—	—	—	—	—

TABLE 6 (*contd.*)

8. Maxillary						
— bent upper and lower arms	+	+	+	+	+	+
— sharp tip of upper arm	—	—	—	+	—	—
— sharp middle process	—	—	—	+	—	—
— straight lower arm	—	—	—	—	—	—
9. Dentary						
— inconspicuous teeth	—	—	—	—	—	—
— well developed teeth	—	—	—	—	—	—
10. Entopterygoid						
— conspicuous lower process	+	+	—	—	—	—
11. Opercle						
— prominent process at upper poster corner	—	—	+	—	+	—
12. Preopercle						
— sharp projection on lower arm	—	—	+	—	—	—
— prominent serrations on ventral margin	—	—	—	—	—	—

	L. daura	*L. blochi*	*L. brevi-rostris*	*L. leuci-scus*	*L. berbis*	*L. lineo-latus*
7. Premaxillary						
— inner process large	—	—	+	—	—	—
— inconspicuous teeth	+	+	—	—	—	—
— prominent teeth	—	—	—	—	—	—
8. Maxillary						
— bent upper and lower arms	+	+	+	+	+	+
— sharp tip of upper arm	—	+	+	+	+	+
— sharp middle process	+	—	—	—	—	—
— straight lower arm	—	—	—	—	—	—

9. Dentary						
— inconspicuous teeth	+	+	—	—	—	—
— well developed teeth	—	—	—	—	—	—
10. Entopterygoid						
— conspicuous lower process	—	—	—	—	—	—
11. Opercle						
— prominent process at upper poster corner	+	—	—	—	—	—
12. Preopercle						
— sharp projection on lower arm	+	—	—	—	—	—
— prominent serrations on ventral margin	—	—	—	—	—	—

	L. bindus	*S. ruconius*	*S. insidiator*	*G. minuta*	*G. achlamys*
7. Premaxillary					
— inner process large	—	—	—	+	+
— inconspicuous teeth	—	+	+	—	—
— prominent teeth	—	—	—	+	+
8. Maxillary					
— bent upper and lower arms	—	—	—	—	—
— sharp tip of upper arm	—	—	—	—	—
— sharp middle process	+	—	—	+	+
— straight lower arm	+	—	—	+	+
9. Dentary					
— inconspicuous teeth	—	—	—	—	—
— well developed teeth	—	—	—	+	+
10. Entopterygoid					
— conspicuous lower process	—	—	—	—	—
11. Opercle					
— prominent process at upper poster corner	—	+	+	—	—
12. Preopercle					
— sharp projection on lower arm	—	—	—	—	—
— prominent serrations on ventral margin	—	—	—	+	+

TABLE 6 (*contd.*)

Character	*L. fasciatus*	*L. equulus*	*L. smithursti*	*L. splendens*	*L. jonesi*	*L. dussumieri*
13. Hyomandibular						
— lower part rod-like	—	—	—	—	—	—
14. Branchiostegal rays						
— five	+	+	+	—	—	—
— four	—	—	—	+	+	+
15. Origin of branchiostegal rays						
— last from epihyal	—	—	—	—	—	—
— last two from epihyal	+	—	+	—	—	—
— all from ceratohyal	—	+	—	+	+	+
16. Third hypobranchial						
— simple	—	—	—	—	+	—
— leaf-like	+	+	+	+	—	+

Character	*L. daura*	*L. blochi*	*L. brevirostris*	*L. leuciscus*	*L. berbis*	*L. lineolatus*
13. Hyomandibular						
— lower part rod-like	—	—	—	—	—	—
14. Branchiostegal rays						
— five	+	—	—	—	—	—
— four	—	+	+	+	+	+
15. Origin of branchiostegal rays						
— last from epihyal	—	—	—	—	—	—
— last two from epihyal	—	+	—	—	—	—
— all from ceratohyal	+	—	+	+	+	+
16. Third hypobranchial						
— simple	—	—	—	+	—	—
— leaf-like	+	+	+	—	+	+

	L. bindus	*S. ruconius*	*S. insidiator*	*G. minuta*	*G. achlamys*
13. Hyomandibular					
— lower part rod-like	—	+	+	—	—
14. Branchiostegal rays					
— five	—	—	—	+	+
— four	+	+	+	—	—
15. Origin of branchiostegal rays					
— last from epihyal	—	—	—	—	—
— last two from epihyal	—	—	—	—	—
— all from ceratohyal	+	+	+	+	+
16. Third hypobranchial					
— simple	+	—	—	—	—
— leaf-like	—	+	+	+	+

L. berbis and *L. lineolatus* resemble one another in the deeply forked anterior end of vomer, small nuchal spine, conspicuous bifid posterior end of parasphenoid, blunt and stumpy epiotic process, bent upper and lower arms of maxillary and the sharp tip of upper arm of maxillary.

While *L. daura, L. blochi* and *L. brevirostris* share only a few characters like the blunt and stumpy epiotic process and bent upper and lower arms of the maxillary, *L. daura* is equally closer to *L. blochi* and *L. brevirostris* in addition to the common characters mentioned above, in the inconspicuous teeth of the premaxillary and the dentary with *L. blochi* and in the conspicuous bifid posterior end of parasphenoid and the conspicuously short posterior process with *L. brevirostris.* Apart from the two common characters *L. blochi* and *L. brevirostris* share with *L. daura,* they resemble one another only in one character, namely, the sharp tip of upper arm of the maxillary.

While *L. bindus* shares the common character of the blunt and stumpy epiotic process with *L. smithursti, L. splendens* and *L. dussumieri,* it shows affinity on one hand to *S. ruconius* and *S. insidiator* in the anterior end of parasphenoid pointing upwards and on the other to *G. minuta* and *G. achlamys* in the sharp middle process and straight lower arm of the maxillary thus appearing to represent a link between the genera *Leiognathus* and *Secutor* on one hand and *Leiognathus* and *Gazza* on the other hand. However, the two species of *Secutor* and the two species of *Gazza* are closer to each other than to species of *Leiognathus* and of *Gazza* in case of species of *Secutor* and to species of *Leiognathus* and of *Secutor* in case of species of *Gazza.*

In the light of this study, the following osteological keys are provided for the genera and species:

Osteological Key to Genera

I. Front half of neurocranium horizontal; nuchal spine small.

1. Parietals rectangular with strong dorsal ridges; upper half of posterior margin of supraoccipital crest crenulated; metapterygoid with anterior and posterior fringes; anterior fringe of hyomandibular prominent, anterior and posterior fringes terminating ventrally at the same point ..... *Leiognathus*

2. Parietals ovoid with delicate dorsal ridges; entire posterior margin of suproaccipital crest wavy; metapterygoid with anterior fringe only; posterior fringe of hyomandibular prominent, terminating below anterior fringe ..... *Gazza*

II. Front half of neurocranium upturned; nuchal spine prominent .. *Secutor*

KEY TO SPECIES OF LEIOGNATHUS

I. Epiotic process not blunt and stumpy.

a1 Anterior end of vomer deeply forked; prominent process at upper posterior corner of opercle ..... *L. jonesi*

a2 Anterior end of vomer not deeply forked; no prominent process at upper posterior corner of opercle.

b1 Epiotic process club-shaped ..... *L. fasciatus*

b2 Epiotic process narrow and sharp ..... *L. equulus*

II. Epiotic process blunt and stumpy

a1 Basisphenoid with conspicuously short posterior process.

b1 Anterior end of vomer deeply forked; sharp projection on lower arm of preopercle ..... *L. smithursti*

b2 Anterior end of vomer not deeply forked; no sharp projection on lower arm of preopercle.

c1 Maxillary without a sharp middle process .... *L. brevirostris*

c2 Maxillary with a sharp middle process.

d1 Lower arm of maxillary straight ..... *L. bindus*

d2 lower arm of maxillary bent.

e1 Teeth on premaxillary and dentary inconspicuous .. *L. daura*

e2 Teeth on premaxillary and dentary clearly visible .... *L. splendens*

a2 Basisphenoid with long posterior process.

f1 Nuchal spine small

g1 Anterior end of vomer deeply forked

h1 Posterior process of basisphenoid bent ..... *L. lineolatus*

h2 Posterior process of basisphenoid not bent .... *L. berbis*

g2 Anterior end of vomer not deeply forked ..... *L. dussumieri*

f2 Nuchal spine big

i1 Teeth on premaxillary and dentary inconspicuous; posterior process of basisphenoid bent ..... *L. blochi*

i2 Teeth on premaxillary and dentary conspicuous, posterior process of basisphenoid not bent ..... *L. leuciscus*

KEY TO SPECIES OF SECUTOR

I. Anterior end of vomer deeply forked; nuchal spine big ..... *S. ruconius*

II. Anterior end of vomer not deeply forked; nuchal spine small ..... *S. insidator*

KEY TO SPECIES OF GAZZA

I. Posterior process of basisphenoid conspicuously short ..... *G. minuta*

II. Posterior process of basisphenoid long ..... *G. achlamys*

The characters of convergence and divergence indicate that within the genus *Leiognathus, L. smithursti, L. splendens, L. jonesi* and *L. dussumieri* appear to be closely related to each other. *L. fasciates* and *L. equulus* form another group. A third group is formed by *L. leuciscus, L. berbis* and *L. lineolatus*. A fourth group is constituted by *L. daura, L. blochi* and *L. brevirostris*. However, *L. bindus* appears to link the genus *Leiognathus* with the other two genera, thus indicating that it is the least evolved of the species of the family. This also indicates perhaps that the genus *Leiognathus* is less evolved compared to the genera *Secutor* and *Gazza*. This contention appears to be supported by the fact that both *Secutor* and *Gazza* exhibit certain specialised characters such as the upward directed protrusible mouth in Secutor and the development of prominent teeth in *Gazza*. In other characters as well, the species of *Secutor* and *Gazza* are widely separated from species of *Leiognathus* and also from one another.

ACKNOWLEDGEMENT

The author is thankful to Mr. Badrudeen, Technical Assistant, Central Marine Fisheries Research Institute, for his able assistance in field work and preparation of osteological material for the study.

REFERENCES

AGASSIZ, L. 1857. Recherches sur les poissons fossiles, Vol. 5 Neuchatel.

BERTIN, L. AND C. ARAMBOURG. 1958b. Super-ordre des Teleosteens (Teleostei), p. 2204-2500. In P. Grasse (ed.) *Traite de Zoologie*, Vol. 13, Masson et Cie, Paris.

BOULENGER, G. A. 1904. *Fishes (Teleostei)*. In S. Harmer, W. Herdman, T. Bridge and G. A. Boulenger (eds.) *Hemicordata, Ascidians*, Fishes.

DELSMAN, G C. 1925. Fishes with prostrusile mouths. *Treubia*, 6: 98-101.

GREGORY, W. K. 1933. Fish skulls; a study of the evolution of natural mechanisms. *Trans. Amer. Phil. Soc.*, (new series): 75-481.

KUSAKA, T. 1974. *The urohyal of fishes*. Univ. of Tokyo Press, Tokyo.

STARKS, E. C. 1911. The osteology and relationships of *Leiognathus*, a genus of Scombroid fishes. *Stanford Univ. Publ., Univ. Ser.* 5: 5-15.

STARKS, E. C. 1926. Bones of the ethmoid region of the fish skull. *Stanford Univ. Publ, Ser. Biol. Sci.*. 5(3): 139-338.

WHITEHEAD, P. J. P. 1975. *How fishes live*. Elsevier-Phaidon, London.