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PHYLOGENY AND BIOGEOGRAPHY OF THE OSTRACIINAE (TETRAODONTIFORMES: OSTRACIIDAE)

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ABSTRACT

Approximately 140 potential phylogenetic characters were recognized to vary among 19 species of ostraciines studied. Phylogenetic relationships were reconstructed on the basis of 108 characters (127 derived states). Two equally parsimonious cladograms of 158 steps, consistency index = 80%, retention index = 94%, were generated. Of the characters used in the analysis, 27 were hypothesized to display homoplastic states; of these, 10 showed no particular trend, 4 hypothesized an alternative resolution within *Lactoria,* and 13 are interpretable as reversals. Two characters were treated as unordered, thus not used in the analysis. Hypotheses of reduction are considered important in ostraciine evolution but do not constitute the dominant explanation for character evolution. Results indicated that ostraciines are monophyletic, consisting of two monophyletic subgroups, the Atlantic *Acanthostracion* and *Lactophrys,* and the Indo-Pacific *Ostracion* and *Lactoria. Acanthostracion* and *Lactophrys* are both monophyletic. *Rhynchostracion* is considered a junior synonym of *Ostracion* (six species) and *Tetrosomus* is considered a junior synonym of *Lactoria* (six species). In both cases recognition of the former genus would render the latter paraphyletic. Much of ostraciine distribution is sympatric. Two sister area relationships are evident: Caribbean/eastern Atlantic and Atlantic/Indo-Pacific.

> "One of the most prominent trends in the evolution of the plectognath [tetraodontiform] fishes has been the reduction through loss or fusion in the number of bony parts, and if this trend has been continued by the trunkfishes, as it probably has, it is apparent that the aracanins are more generalized, and presumedly more primitive, than the ostraciontids." (Tyler, 1963: 188)

Several authors have studied higher level relationships within the Tetraodontiformes based on osteology (Rosén, 1916; Gregory, 1933; Breder and Clark, 1947; Tyler, 1968, 1980; Matsuura, 1979; Winterbottom and Tyler, 1983; Arai, 1983; Rosen, 1984), myology (Winterbottom, 1974; Winterbottom and Tyler, 1983), softbody anatomy (Breder and Clark, 1947; Mok, 1974), larval and juvenile characters (Breder and Clark, 1947; Leis, 1984), and karyology (Arai, 1983). At least among those studying osteological characters, there is agreement that reduction has played some role in tetraodontiform evolution. Three general phylogenetic schemes for the relationships of ostraciids to other tetraodontiforms have been proposed (Fig. 1). Breder and Clark (1947) considered the Ostraciidae to have arisen basally within the Tetraodontiformes. Rosen (1984) and Leis (1984) placed the Ostraciidae in the Tetraodontoidea. Rosen (1984) based his conclusion on a single osteological character (dorsal fins and radials [pterygiophores] remote from occipital region of skull). Leis (1984) based his conclusion on a series of 14 early life history characters. Gregory (1933), Winterbottom (1974), Matsuura (1979), Tyler (1980), and Winterbottom and Tyler (1983) proposed that the Ostraciidae belong in the Balistoidea as the sister group to the Balistidae. Combined osteological and myological evidence indicates that a total of 20 characters support the latter hypothesis (Winterbottom and Tyler, 1983). Winterbottom and Tyler (1983) also provided evidence for monophyly of the two Ostraciidae subfamilies, Ostraciinae and Aracaninae; they did not further discuss relationships within the Ostraciinae. Indeed, very few workers have focused on generic level relationships within the Tetraodontiformes; cladistic treatment is limited to the studies of Mat-

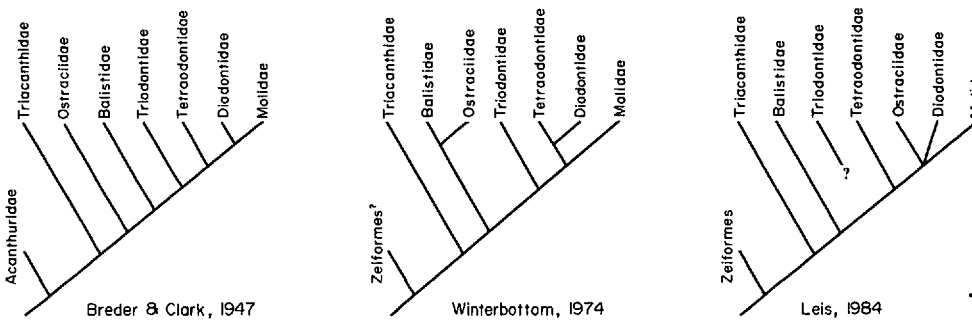

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Figure 1. Alternate hypotheses of familial relationships within the Tetraodontiformes. The tree by Breder and Clark (1947) was not originally presented as a cladogram. Although Winterbottom (1974) did not explicitly use zeiforms as outgroup, he implied that they should be. The Triacanthodidae are left out for consistency because it was not considered by Breder and Clark (1947).

suura (1979) on Balistidae relationships and Winterbottom and Tyler (1983) for Aracaninae relationships. Tyler (1980) did present a non-cladistic scheme of relationships for Ostraciinae genera: (((*Ostracion* + *Rhynchostracion*) + (*Lactoria* + *Tetrosomus*)) + (*Acanthostracion* + *Lactophyrys*)). A detailed cladistic treatment of species level relationships is still lacking for all tetraodontiform taxa.

> "An understanding of the progressive stages in the modification of the ostraciontoid vertebral column will undoubtedly play an important role in deciphering the phylogeny of the trunkfishes in the absence of an adequate fossil record, and strengthen the diagnosis of the families and subfamilies and perhaps even the genera within the suborder." (Tyler, 1963: 187–188)

Tyler predicted that reduction would be a major force in the evolution of ostraciine relationships, and that study of the vertebral column, in particular, has been most important in shaping interpretations of phylogenetic relationships. He has emphasized this belief in further studies on the fusion characteristics of the anteriormost abdominal vertebrae, and modifications to the posterior caudal vertebrae and centrum-hypural plate (Tyler, 1963, 1970). Most of this work was based on specimens of 'representative' species, especially *Acanthostracion quadricornis,* even though Tyler recognized that this species may not be so representative after all (i.e., many of its morphological characters are autapomorphic). Furthermore, Tyler's work was explicitly non-cladistic (and his represents the vast majority of osteological work conducted on ostraciine species). Tyler considered both plesiomorphic and apomorphic characters as important in reconstructing phylogenetic relationships.

Very little is known about the geographic distribution of ostraciines and, with the exception of some tentative remarks by Tyler (1980), even less is known about their historical biogeography. Tyler's conclusions about historical relationships rely on fossil data and the implicit assumption that fossils by definition are older than, and therefore ancestral to, extant taxa.

The goal of the present study is therefore fourfold. (1) To conduct an analysis of the species level phylogenetic relationships of ostraciines based on their osteology. (2) To examine questions of character evolution: interpreting homoplasy, the problem of polarizing multistate characters, as well as the importance of character complexes. Is reduction a dominant trend in the phylogenetic relationships among ostraciine taxa? (3) To reevaluate generic level taxonomy in a phylogenetic context. (4) To combine those data with distribution data to address questions of ostraciine historical biogeography.

MATERIALS AND METHODS

Nineteen species of Ostraciinae were examined (Appendix 1; *Ostracion trachys* was not examined due to the paucity of available specimens). Cleared and stained material for ingroup and outgroup specimens was obtained from three sources (Appendix 2): ANSP (Academy of Natural Science of Philadelphia; I am particularly grateful to Jim Tyler, who cleared and stained this material), ROM (Royal Ontario Museum, Toronto), and USNM (National Museum of Natural History, Collections formerly in the United States National Museum, Washington, D.C.). Additionally extensive use was made of the excellent osteological work of Tyler (1963, 1965a, 1965b, 1968, 1970, 1980), which provided an invaluable source of data for both ingroup and outgroup comparisons. When stained material was not available, additional specimens were cleared and stained according to standard techniques (Dingerkus and Uhler, 1977; Taylor and Van Dyke, 1985). Each of 69 cleared and stained bones/bone groups in 13 body regions (sensu Tyler, 1980) was examined under a Wild M5A dissecting microscope, and drawings made with the aid of a camera lucida.

One hundred and forty potential characters (both binary and multistate) were identified. Of these, 31 were discarded as either too variable to be polarized or invariant in the ingroup. The remaining characters and their states were described and depicted (Table 1, Figs. 2–31). Character state polarization for binary characters was accomplished by the outgroup polarization method of Watrous and Wheeler (1981, see also Maddison et al., 1984). A paraphyletic series of outgroups was used according to the phylogenies of Winterbottom (1974) and Winterbottom and Tyler (1983), with Aracaninae as the immediate sister group and Balistidae, Tetraodontidae (+ Diodontidae), Triacanthidae (+ Triacanthodidae) sequentially more distantly related. Multistate characters were treated in two ways. Initially, they were coded as linear transformation series (i.e., treated as "ordered"). Subsequently, these characters were coded as unordered and the results compared. Character states were coded for phylogenetic analysis (Table 2). A preliminary cladogram for the ingroup was generated by hand, based on character state polarity decisions as represented in Table 2. This was compared to computerized analyses conducted with HENNIG'86 v1.5 (available from J. S. Farris). Due to the size of the data set, the 'mhennig*' and 'bb' options were used to estimate most parsimonious trees.

For the biogeographic study, material was examined at the following museums: ANSP, CAS (California Academy of Sciences), ROM, USNM, ZUMT (University Museum, Tokyo); additional museum records were obtained from AMNH (American Museum of Natural History, New York), AMS (Australian Museum, Sidney), BMNH (British Museum of Natural History, London), BPBM (Bishop Museum, Honolulu), LACM (Natural History Museum of L.A. County, Los Angles), MNHN (Museum National d'Histoire Naturelle, Paris), NTM (Museum and Art Galleries of the Northern Territory, Darwin), RUSI (Smith Institute, Rhodes University of Ichthyology, Grahamstown), SMF (Forschungsinstitute Senkengerg, Frankfurt), TAU (University Museum, Tel Aviv), UMMZ (University of Michigan Museum of Zoology, Ann Arbor), WAM (Western Australian Museum, Perth), ZMUC (Zoologisk Museum, Copenhagen), and literature records from Bölke and Chaplin (1993), Masuda (1984), Myers (1989), Okamura et al. (1985), Randall (1983), Randall et al. (1990), Smith (1961), Thomson et al. (1979), Tyler (1965a, 1965b).

RESULTS

(1) Taxonomic History

The taxonomic history of the Ostraciinae (sensu Winterbottom, 1974, whose scheme of higher classification will be followed throughout) is long and complex. Linnaeus's (1758) "Systema Naturae," the first officially recognized taxonomic record for ostraciine boxfishes, summarized the work of previous authors (Artedi, Willoughby, Gronovius) and included all boxfishes in *Ostracion,* which he placed in the Branchiostegi (hidden gills). He recognized nine species. *O. triqueter, O. trigonus, O. bicaudalis, O. tricornis, O. quadricornis, O. cornutus, O. tuberculatus, O. gibbosus,* and *O. cubicus.* In the 12th edition of the Systema Naturae, Linnaeus (1766) did not use the Branchiostegi; instead, he placed *Ostracion* in the Amphibia Natantes (swimming amphibians). In the 13th edition (1788), he once again included *Ostracion* in the reinstated Branchiostegi. Since then many nominal species have been described and the number of recognized genera has

Table 1. Summary of bones examined (ordered by group sensu Tyler, 1980), number of polarizable characters and number of states per character

Bones examined	Group	Characters (No.)	States (No.)
Basioccipital	occipital	none (invariant)	0
Exoccipital	occipital	one	1
Supraoccipital	occipital	three	1, 1, 1
Pterotic	otic	one	1
Sphenotic	otic	four	1, 1, 1, 1
Epiotic	otic	two	1, 1
Prootic	otic	four	1, 2, 1, 1
Frontal	orbital	two	1, 2
Lateral ethmoid	orbital	six	1, 1, 1, 1, 1, 1
Parasphenoid	orbital	three	2, 1, 1
Pterosphenoid	orbital	two	1, 2
Ethmoid	ethmoid	four	1, 2, 1, 1
Vomer	ethmoid	none (invariant)	0
Hyomandibula	suspensorium	five	1, 1, 1, 1, 1
Quadrate	suspensorium	none	0
Metapterygoid	suspensorium	none	0
Symplectic	suspensorium	one	1
Palatine	suspensorium	none	0
Ectopterygoid	suspensorium	one	1
Mesopterygoid	suspensorium	one	1
Operculum	suspensorium	two	2, 1
Subopercle	suspensorium	two	1, 1
Interopercle	suspensorium	none	0
Preopercle	suspensorium	one	1
Premaxilla	jaw	none	0
Maxilla	jaw	none	0
Dentary	jaw	none	0
Angulo-articular	jaw	none	0
Retroarticular	jaw	none	0
Hypohyals	branchial app.	none	0
Ceratohyals	branchial app.	none	0
Epihyals	branchial app.	two	1, 1
Interhyals	branchial app.	none	0
Branchiostegal rays	branchial app.	one	1
Urohyal	branchial app.	none	0
Basibranchials	branchial app.	none	0
Hypobranchials	branchial app.	none	0
Ceratobranchials	branchial app.	none	0
Epibranchials	branchial app.	none	0
Pharyngobranchials	branchial app.	three	1, 1, 1
Posttemporal	pectoral	none	0
Baudelot's ligament	pectoral	one	3*
Supracleithrum	pectoral	none	0
Cleithrum	pectoral	three	2, 3*, 1
Postcleithra	pectoral	one	1
Coracoid	pectoral	two	1, 1
Scapula	pectoral	none	0
Actinosts	pectoral	none	0
Fin rays	pectoral	none	0
#1	abdominal vertebrae	none	0
#2	abdominal vertebrae	one	1
#3	abdominal vertebrae	four	1, 1, 1, 1
#4	abdominal vertebrae	three	1, 1, 1
#5	abdominal vertebrae	three	1, 1, 1
#6	abdominal vertebrae	none	0
#7	abdominal vertebrae	none	0
#8	abdominal vertebrae	none	0
#9	abdominal vertebrae	none	0

Table 1. Continued

Bones examined	Group	Characters (No.)	States (No.)
#1	caudal vertebrae	none	0
#2	caudal vertebrae	none	0
#3	caudal vertebrae	two	2, 1
#4	caudal vertebrae	five	2, 1, 1, 1, 1
#5	caudal vertebrae	seven	1, 2, 2, 2, 1, 1, 1
#6	caudal vertebrae	six	1, 1, 2, 1, 2, 1
#7	caudal vertebrae	two	2, 1
#8	caudal vertebrae	three	2, 1
Centrum-hypural plate		four	1, 1, 1, 1
Dorsal fin		three	2, 1, 1
Anal fin		seven	1, 1, 1, 1, 1, 1, 1
		108	127

* Character state transformation treated as unordered.

expanded. Until today, six genera (*Acanthostracion, Lactophrys, Lactoria, Tetrosomus, Ostracion,* and *Rhynchostracion*) containing a total of 20 species (depending on authority) have been recognized (Appendix 1).

(2) Characters

In studying the osteology of the 19 ostraciine species, 108 usable characters are recognized (90 binary + 18 multistate = 127 derived binary states). Table 1 summarizes the distribution of characters and their states (including bones found to lack usable characters). Character distribution and polarization decisions are presented below; "0" indicates plesiomorphic state, "1" or higher indicates apomorphic state (see Table 2). Description of state distribution is followed by comments where appropriate.

Skull: Occipital Region

1—Exoccipitals Dorsally Separated by Cartilage (Fig. 2).—In Indo-Pacific boxfishes and the outgroup taxa this bone is wide and meets its opposite member, forming the dorsal surface of the foramen magnum (0). In Atlantic boxfishes this bone is narrower and is separated from its opposite member by a cartilage-filled gap equal to (and contiguous with) the gap separating the dorsal extent of the neural arches of the first three fused abdominal vertebrae (1).

Tyler mentioned that in *Acanthostracion quadricornis* the dorsal regions of the exoccipitals were separated posteriorly by "fibrous tissue," but anteriorly by "a thin sheet of cartilage" (Tyler, 1980: figs. 151, 152). I was unable to confirm this distinction between anterior and posterior separations. Tyler also depicted separated dorsal elements for *Rhynchostracion rhinorhynchus* (Tyler, 1980: fig. 176). The material I examined leads me to disagree with that interpretation.

2—Supraoccipital Crest Absent (Fig. 2).—A crest is present in all outgroup taxa (0). The crest is absent in all ingroup taxa (1).

Most, but not all, ostraciines retain the plesiomorphic transverse ridge also found in Aracaninae. Presence of this ridge varies both among and within taxa; it thus appears too variable to provide phylogenetic information.

3—Anterior Margin of Supraoccipital Lacking Triangular Wedge (Fig. 2).—In the outgroup taxa and most ostraciines, the supraoccipital is pointed anteriorly, inserting a triangular wedge partway between the posteromedial margins of the

Table 2. Character state matrix for Ostraciinae: T. = Tetraodontidae, B. = Balistidae, A. = Aracaninae (these together form the paraphyletic outgroup), Ap = *Acanthostracion polygonius,* Aq = *A. quadricornis,* An = *A. notacanthus,* Ag = *A. guineaensis,* Lb = *Lactophrys bicaudalis,* Lg = *L. trigonus,* Lq = *L. triqueter,* Ld = *Lactoria diaphana,* Lf = *L. fornasini,* Lc = *L. cornuta,* Om = *Ostracion meleagris,* Oy = *O. cyanurus,* Ou = *O. cubicus,* Ow = *O. whitleyi,* Rn = *Rhynchostracion nasus,* Rr = *R. rhinorhynchus,* Tr = *Tetrosomus republicae,* Tg = *T. gibbosus,* Tc = *T. concatenatus.* '/' indicates states in outgroup taxa not found in the ingroup. '?' indicated missing data

Char. (no)	T.	B.	A.	Ap	Aq	An	Ag	Lb	Lq	Lg	Om	Oy	Ou	Ow	Rn	Rr	Ld	Lc	Lf	Tr	Tg	Tc
1	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	/	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
6	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
7	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1
8	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
10	/	/	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	/	/	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
12	/	/	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
13	/	/	0	0	0	0	0	0	0	0	1	1	1	1	2	2	1	1	1	1	1	1
14	/	/	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
15	/	/	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
17	0	0	0	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
18	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?	0	0	0
21	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
24	0	0	0	1	1	2	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	/	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0
27	/	/	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
28	/	/	0	0	0	0	0	0	0	0	1	2	2	2	1	1	1	1	1	1	1	1
29	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
33	/	/	0	1	1	1	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
35	/	/	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
36	/	/	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
38	/	0	0	0	0	0	0	0	0	0	?	1	?	1	?	?	1	1	1	?	1	1
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
40	/	/	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0
41	0	0	0	1	1	1	1	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
43	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
45	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
46	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	1	1	?	1	1	1	0	0	0	1	1	1
48	/	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
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50	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
51	/	/	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	?	?	1	0	0
52	/	/	0	1	1	1	1	1	1	1	3	3	3	3	3	3	1	2	?	1	2	1
53	0	0	0	0	0	0	0	0	0	0	?	2	2	2	2	2	1	1	1	1	1	1

Table 2. Continued

Char. (no)	T.	B.	A.	Ap	Aq	An	Ag	Lb	Lq	Lg	Om	Oy	Ou	Ow	Rn	Rr	Ld	Lc	Lf	Tr	Tg	Tc
54	0	0	0	3	3	3	3	2	2	2	0	0	0	0	0	0	1	1	1	1	1	1
55	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1
56	/	/	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
57	/	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0
59	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
60	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1
61	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
62	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
63	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1
64	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
65	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
67	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
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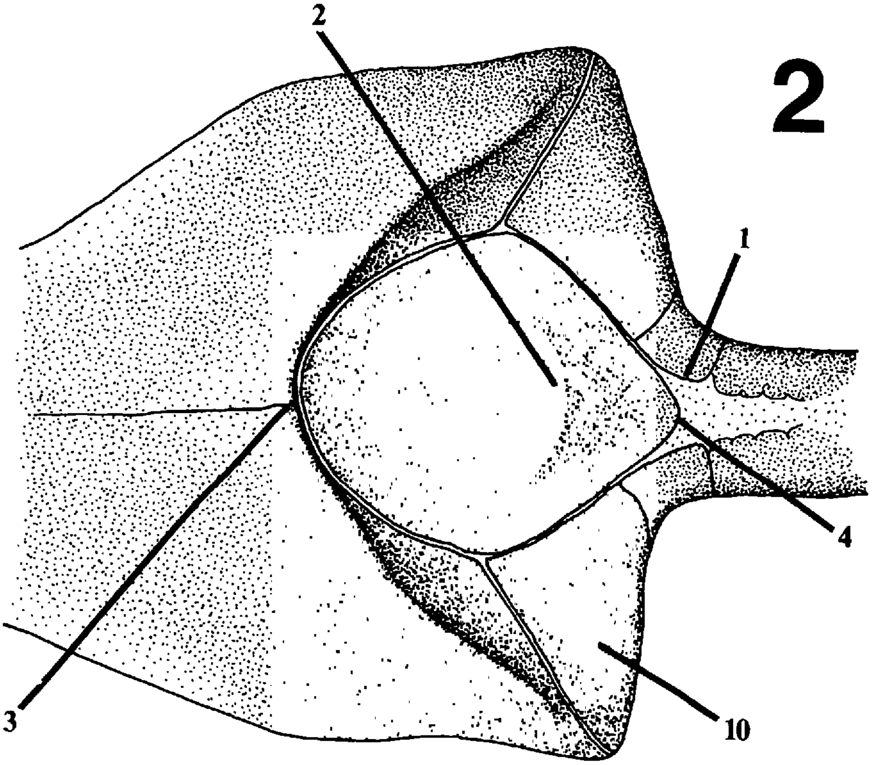


Figure 2. Skull of *Acanthostracion guineaensis*, dorsal view of occipital region: (1) indicates exoccipitals dorsally separated; (2) absence of supraoccipital crest; (3) absence of anteriorly directed supraoccipital wedge; (4) supraoccipital with posterior wedge between exoccipitals; (10) epiotic crest absent.

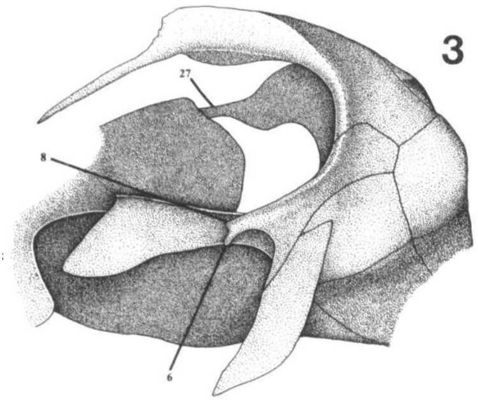
frontals (0). In *Acanthostracion notacanthus* and *A. guineaensis* the wedge is absent, such that the posterior margin of the frontals provides an unbroken transverse ridge (1).

4—Posterior Margin of Supraoccipital with Triangular Wedge Between Exoccipitals (Fig. 2).—In the outgroup taxa and most ostraciines the exoccipitals meet dorsally (see character 1) and the supraoccipital does not form a posteriorly directed wedge between them (0). In *Acanthostracion notacanthus* and *A. guineaensis* the posteromedian margin of the supraoccipital is posteriorly expanded to form a triangular wedge between the exoccipitals (1).

Skull: Otic Region

5—Pterotic Shaft Expanded Laterally.—The lateral region of the pterotic is expanded into a ventrally directed shaft in all balistoids but not tetraodontoids or triacanthoids (0). In *Ostracion* and *Rhynchostracion* species this shaft is expanded laterally forming a dorsolateral strut which supports the orbit posterolaterally (1).

Tyler (1980) observed that the ventrally directed shaft is usually obscured by the posttemporal to which it is joined by fibrous tissue and/or interdigitation. I was unable to confirm the latter observation.



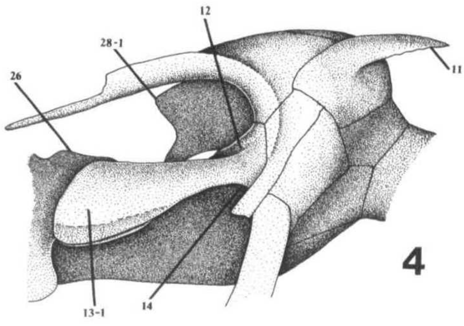


Figure 3 (left). Skull of *Acanthostracion polygonius,* lateral view of posterior half: (6) ventral projection of sphenotic ridge; (8) anterior projection of sphenotic ridge; (27) fusion of pterosphenoid projection to midorbital keel of parasphenoid.

Figure 4 (right). Skull of *Ostracion cubicus,* lateral view of posterior half: (11) horizontal epiotic crest; (12) anteriorly expanded posterior surface of prootic; (13-1) prootic shelf angled ventrolaterally; (14) reduction of ventral keel of prootic shelf; (26) reduced midorbital keel of parasphenoid; (28-1) reduced pterosphenoid projection.

6—Sphenotic Ridge with Ventral Projection (Fig. 3).— In the outgroup taxa and most ostraciines, the sphenotic is thickened along its anterior edge into a ridge which together with a similar thickening of the frontals forms the posterodorsal support for the lateral margin of the orbit (0; Fig 4). In *Acanthostracion polygonius* and *Lactoria* species the distal tip of the ridge has a ventral process to which inserts the ligament from the lateral surface of the hyomandibula (1).

7—Sphenotic Ridge Expanded Laterally.—In the outgroup taxa and several ostraciines the sphenotic ridge is narrow along its dorsal surface (0). In *Acanthostracion quadricornis, A. notacanthus, A. guineaensis,* and *Tetrosomus gibbosus, T. concatenatus* and *Rhynchostracion* species the sphenotic ridge is expanded laterally to form a broad shelf (1).

8—Sphenotic Forms Ventral Extension of Orbital Ridge (Fig. 3).—In the outgroup taxa and most ostraciines the sphenotic extends ventrally but not anteriorly (0; Fig. 4). In *Acanthostracion* species the ventral tip of the ridge is expanded anteriorly to form a ventral extension of the orbital ridge (1).

9—Sphenotic Expanded Dorsally.—In the outgroup taxa and Atlantic ostraciines the sphenotic is situated laterally on the skull (0). In Indo-Pacific ostraciines the sphenotic is expanded dorsally to form part of the dorsal surface of the skull (1).

This is further modified in *Ostracion* and *Rhynchostracion* species to form, together with the pterotic, the lateral strut. This further modification of the sphenotic is not considered an independent character.

10—Absence of Epiotic Crest (Fig. 2, see also Fig. 3).—Most ostraciine species share with Aracaninae the presence of a roughly vertical crest arising from a median ridge bisecting the bone (0; the remaining outgroup taxa lack a homologous condition). *Acanthostracion* species have lost the crest entirely, with only a ridge visible where the crest would have been (1).

Winterbottom and Tyler (1983) describe a 'strong posterolateral process' arising from the epiotics of Aracaninae to be autapomorphic for that group, with the lack of such a process as the primitive condition. If their process is homologous with the crest described here (and I see no reason to doubt this interpretation), their character may be interpreted as the second step in a transformation series beginning with the development of the crest. Alternatively, the crest of ostraciines is derived from the posterolateral process of Winterbottom and Tyler (1983); in either case the crest/process must be interpreted as derived for the Ostraciidae as a whole and not just for the Aracaninae as they proposed.

11—Epiotic Crest Horizontal (Fig. 4).—In Aracaninae and those remaining ostraciines with a crest, the crest is vertical (0; the remaining outgroup taxa lack a homologous condition). In *Ostracion* and *Rhynchostracion* species the crest has moved to a horizontal position on the dorsolateral surface of the epiotic (1).

This reorientation is possibly a response to an overall outward expansion of the lateral and dorsolateral surfaces of the cranium in these taxa.

12—Posterior Surface of Prootic Expanded Anteriorly (Fig. 4).—In Aracaninae, *Acanthostracion* and *Lactophrys* species, the posterior part of the prootic is more or less vertical, forming the ventral half of the posterior orbital support (0; the remaining outgroup taxa lack a homologous condition). In all Indo-Pacific ostraciines this component has expanded anteriorly so that support for the orbit is shifted ventromedially and a larger surface of contact with the hyomandibula is provided (1).

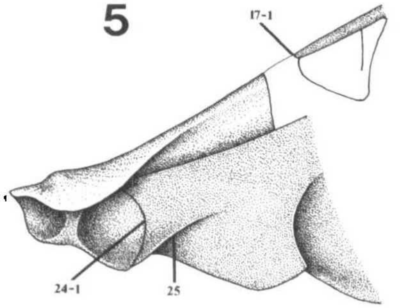
Although all tetraodontiforms appear to possess an anteromedian process, only Ostraciidae have it modified into a suborbital shelf with a ventral keel.

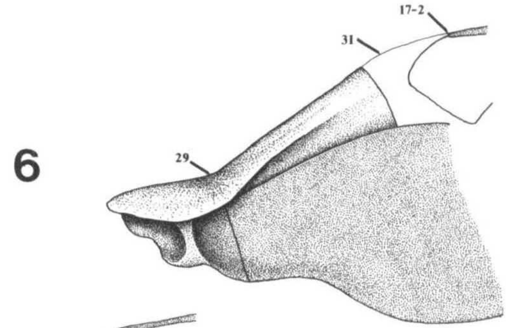
13—Modified Suborbital Shelf of Prootic (Fig. 4).—Aracanines and Atlantic ostraciines have a simple, horizontal suborbital shelf (0; no homologous condition exists for the other outgroup taxa). Indo-Pacific ostraciines have the suborbital shelf modified, such that it is no longer horizontal but angled ventrally at approximately 30–40 degrees from the horizontal (1). Furthermore, *Rhynchostracion* species have partly fused the gap between the shelf and ventral keel forming a short channel (2).

14—Ventral Keel of Suborbital Shelf Reduced (Fig. 4).—The ventral keel of the prootic shelf of Aracaninae and the Atlantic ostraciines bears two distinct processes, one anteroventral, the other posteroventral (0; Fig. 3, no homologous condition exists for the other outgroup taxa). In Indo-Pacific ostraciines the entire keel is reduced so that neither process is clearly visible and the associated foramen is always open (1).

The posteroventral process of aracanines and ostraciines may be connected by fibrous tissue to the ventromedial edge of the posterior component of the prootic forming a foramen (this varies a great deal depending on stage of development and was observed consistently only for *A. polygonius*). Winterbottom and Tyler (1983) interpreted the keel with anterior and posterior processes to be autapomorphic for Aracaninae. The present analysis indicates that the most parsimonious interpretation implies this morphology is synapomorphic for Ostraciidae as a whole (Aracaninae plus Ostraciinae).

15—Large Gap between Prootic Shelf and Parasphenoid.—In Aracaninae, *Acanthostracion* species and Indo-Pacific ostraciines there is a small gap in the ventromedian joint between the prootic shelf and parasphenoid (0; no homologous condition exists for the other outgroup taxa). This gap is enlarged, both laterally and posteriorly in *Lactophrys* species (1).





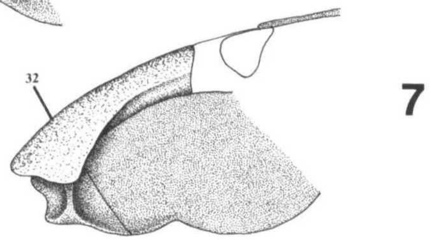


Figure 5. Skull of *Acanthostracion polygonius*, lateral view of anterior half: (17-1) anterior extent of frontals contacts ethmoid cartilage; (24-1) frontal-vomer junction posteriorly convex; (25) anterolateral ridge on parasphenoid.

Figure 6. Skull of *Lactoria diaphana*, lateral view of anterior half: (17-2) anterior extent of frontals contacts dorsomedian surface of lateral ethmoid; (29) ethmoid indented at junction between blade and shaft; (31) convex bend at ethmoid cartilage.

Figure 7. Skull of *Ostracion rhinorhynchus*, lateral view of anterior half: (32) 'spongy' expansion of ethmoid blade.

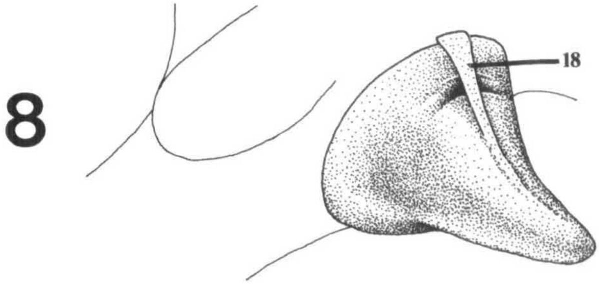
Skull: Orbital Region

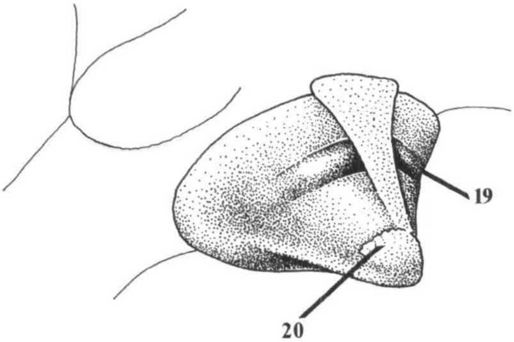
16—Frontals Form Distinct Arch over Orbits.—In the outgroup taxa and most ostraciine species a pair of thin supraorbital expansions is present, joined by fibrous tissue to the carapace (0). In *Lactoria* and *Tetrosomus* species the supraorbital expansion is strongly deflected dorsolaterally to form a distinct arch over the orbital region (1).

17—Modification to Anterior Extent of Frontals (Figs. 5, 6; see also Fig. 7).—In the outgroup taxa the anterior projections of the frontals extend anteriorly to overlie the ethmoid in addition to ethmoid cartilage and lateral ethmoids (0). In all ostraciines these projections have been reduced. A two state transformation is observed. In Atlantic ostraciines the anterior extent of the projections overlies the lateral ethmoids and makes contact with the ethmoid cartilage (1). In all Indo-Pacific ostraciines the anterior edge of the projections makes contact with the dorsomedian surface of the lateral ethmoids but never reaches the ethmoid cartilage (2).

Winterbottom and Tyler (1983) interpreted the anterior projections of the frontals extending anteriorly to overlie the ethmoid in addition to ethmoid cartilage and lateral ethmoids to be autapomorphic for the Aracaninae.

18—Lateral Ethmoid Ridge Narrow along Entire Length (Fig. 8).—In the outgroup taxa and most ostraciines, these bones possess on their dorsolateral surface a posteroventrally angling groove from mid-dorsal surface to posterodorsal edge (somewhat medial). This groove is partially covered by a ridge of bone arising from the distal point, passing medially where it expands and joins medially to





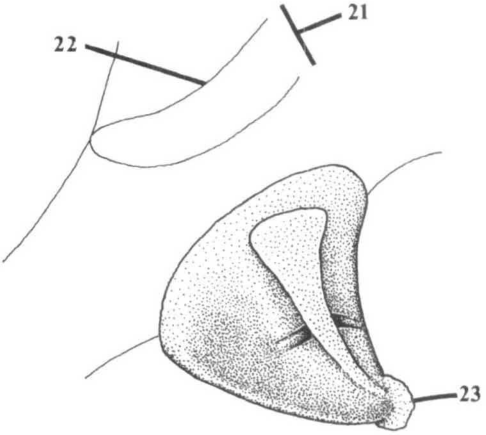


Figure 8. Lateral ethmoid of *Acanthostracion polygonius*, anterolateral view: (18) narrow dorsomedian ridge.

Figure 9. Lateral ethmoid of *Lactoria diaphana*, anterolateral view: (19) dorsolateral groove under ridge; (20) ridge on distal tip.

Figure 10. Lateral ethmoid of *Ostracion cubicus*, anterolateral view: (21) dorsoventral flattening; (22) convex rounding of median surface; (23) posterolateral flange.

the ethmoid cartilage and dorsally to the frontal (0). In *Acanthostracion* species this ridge of bone is narrow along its entire length (1).

19—Lateral Ethmoid Groove More Lateral in Position (Fig. 9).—In the outgroup taxa and most ostraciines the lateral ethmoid groove is close to the median edge of the bone (0; see Fig. 8). In *Lactoria* and *Tetrosomus* species the median portion of the bone has expanded laterally resulting in an elongated bone with the groove more lateral in position (1).

20—Lateral Ethmoids with Medially Directed Distal Ridge (Fig. 9).—The outgroup taxa and most ostraciines lack a medially directed ridge on the dorsolateral surface of the lateral ethmoids (0; see Fig. 8). In *Lactoria diaphana* and *L. cornuta* there is, on the distal tip, a ridge of bone directed medially, ending at the groove (1; specimens of *L. fornasini* were inconclusive as to the presence/absence of this character).

21—Lateral Ethmoids Dorsoventrally Flattened (Fig. 10).—In the outgroup taxa and most ostraciines the median contact of the lateral ethmoids with the ethmoid cartilage is fairly deep (0; see Figs. 8, 9). In *Ostracion* and *Rhynchostracion* species the ethmoid is dorsoventrally flattened (1).

22—Median Surface of Lateral Ethmoids Convex (Fig. 10).—In the outgroup taxa and most ostraciines the median surface of the lateral ethmoids is concave (0; see Figs. 8, 9). In *Ostracion* and *Rhynchostracion* species the bone exhibits a convex rounding of the median surface in contact with the ethmoid cartilage (1).

23—Posterolateral Flange on Distal Tip of Lateral Ethmoid (Fig. 10).—In the outgroup taxa and most ostraciines the distal tip of the lateral ethmoid is rounded, lacking a posterolateral flange (0; see Figs. 8, 9). In *Ostracion* and *Rhynchostracion* species a posterolateral flange arises from the distal tip of the bone (1).

24—Modifications to Parasphenoid (Fig. 5).—In the outgroup taxa and Indo-Pacific ostraciines the joint between parasphenoid and vomer is roughly straight, tracing a posteriorly-directed line from anterodorsal to posteroventral (0; see Figs. 6, 7). In Atlantic ostraciines the ventral contact between the two bones is more anterior so that in *Acanthostracion polygonius, A. quadricornis,* and *Lactophrys* species the joint line is posteriorly convex (1), and in *A. notacanthus* and *A. guineaensis* it is, additionally, medially pointed (2).

25—Parasphenoid with Symmetrical Lateral Ridges (Fig. 5).—In the outgroup taxa and most ostraciine species the anteroventral joint of the parasphenoid with the vomer is not supported by any additional modifications (0; see Figs. 3, 4). In all *Acanthostracion* species the anteroventral joint of the parasphenoid with the vomer is reinforced by symmetrical lateral ridges (1).

26—Dorsal Midorbital Keel of Parasphenoid Reduced (Fig. 7).—In Aracaninae and most ostraciine species the parasphenoid has a distinct midorbital keel (0; the condition for balistids appears non-homologous, the condition for tetraodontids is polymorphic). In *Ostracion* and *Rhynchostracion* species the dorsal, midorbital keel is indistinct (1).

27—Anterior Projections of Pterosphenoids Elongated and Fused (Fig. 3).—In aracanines and many ostraciines a pair of median projections join anterodorsally to contact the posterodorsal surface of the interorbital keel of the parasphenoid (0; no homologous condition is observed in the other outgroup taxa). In Atlantic ostraciines these projections are elongated and thin anteriorly and fuse indistinguishably to one another (1).

28—Reduction of Pterosphenoid Projection (Fig. 4).—In aracanines and many ostraciines a pair of median projections join anterodorsally to contact the posterodorsal surface of the interorbital keel of the parasphenoid (0; no homologous condition is observed in the other outgroup taxa). In all Indo-Pacific ostraciines the contact between the interorbital keel of parasphenoid and pterosphenoid projection is reduced and the projection itself is less conspicuous (1). In *Ostracion cubicus, O. cyanurus,* and *O. whitleyi* the projection is entirely lost (2).

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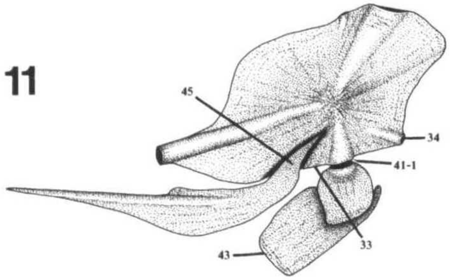

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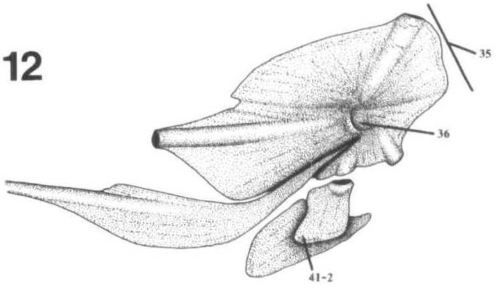

Figure 11 (left). Suspensorium of *Acanthostracion quadricornis*, lateral view of posterior section: (33) opercular process on hyomandibula separated by space from preopercular groove; (34) posteroventral process on hyomandibula; (41-1) broadening of articulating head between opercle and hyomandibula; (43) anteroventral expansion of subopercle; (45) posterior projection of preopercle recurved.

Figure 12 (right). Suspensorium of *Lactophrys bicaudalis*, lateral view of posterior section: (35) dorsoventral compression of hyomandibula; (36) semicircular ridge on midlateral surface of hyomandibula; (41-2) opercular blade expanded anteroventrally.

Skull: Ethmoid Region

29—Concave Indentation between Blade and Shaft of Ethmoid (Fig. 6).—In the outgroup taxa and *Acanthostracion* species the dorsal surface of this bone is smooth and straight (0; see Fig. 8). In *Lactophrys* and Indo-Pacific ostraciines there is an indentation at the junction between blade and shaft (1).

30—Posterior of Ethmoid Shaft Flared.—In the outgroup taxa and most ostraciines the blade is only slightly expanded and the shaft continues more or less straight without flaring (0). In *Lactoria* species the blade is more spade-like, broadened posteriorly at junction with the shaft and narrowing anteriorly; in addition, the posterior part of the shaft is flared slightly (1).

31—Ethmoid/Lateral Ethmoid Junction Concave (Fig. 6).—In the outgroup taxa and most ostraciines the ethmoid/lateral ethmoid junction is smooth and straight (0; see Fig. 5). In *Lactoria* and *Tetrosomus* species there is a concave bend at the level where the ethmoid cartilage meets the lateral ethmoids (1).

32—Ethmoid Blade Expanded (Fig. 7).—In the outgroup taxa and most ostraciines the blade and shaft of the ethmoid are distinct and straight or concave (0). In *Rhynchostracion nasus* the blade is compressed laterally and expanded dorsally pushing up the entire carapace locally; the blade of *R. rhinorhynchus* is similarly expanded, as is the rest of the ethmoid. This expansion results in an enlarged "spongy" structure, which in turn affects the morphology of the carapace (1).

Suspensorium: Mandibular Region

33—Space Separating Opercular Process from Preopercular Groove on Hyomandibula (Fig. 11).—In aracanines and Indo-Pacific ostraciines the opercular process and preopercular groove are situated directly next to one another (0). In *Acanthostracion* species the process to which the opercle articulates is set further posteriorly on the hyomandibula such that a distinct space separates it from the preopercular groove (1; this space appears to be absent in *Lactophrys* species which have, however, undergone several modifications of the hyomandibula, making it difficult to determine polarity).

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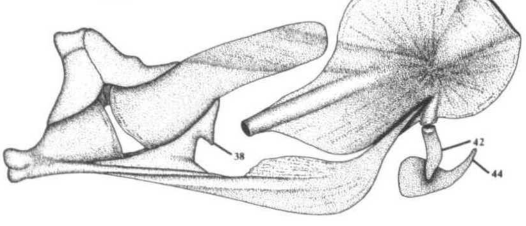

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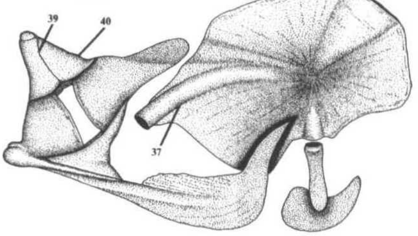

Figure 13 (left). Suspensorium of *Lactoria fornasini*, lateral view: (38) ventral process on symplectic; (42) opercle reduced to thin, flattened shaft; (44) posterior of subopercle expanded to curved point.

Figure 14 (right). Suspensorium of *Ostracion nasus*, lateral view: (37) anterior rod-like process of hyomandibula with ventral curvature; (39) ectopterygoid and mesopterygoid rotated counter-clockwise; (40) mesopterygoid bulge absent.

34—Hyomandibula with Posteroventral Process (Fig. 11).—In the outgroup taxa and Indo-Pacific ostraciines the posteroventral surface of the hyomandibula is rounded, lacking any protrusions (0). Atlantic ostraciines possess a small but distinct process of unknown origin and function on the posteroventral edge of the hyomandibula (1).

35—Hyomandibula Dorsoventrally Flattened (Fig. 12).—In aracanines and most ostraciines the hyomandibula is a large, squarish bone (0; see Fig. 11; no homologous condition is observed in the other outgroup taxa). In *Lactophrys* species the entire hyomandibula is dorsoventrally flattened (1).

36—Hyomandibula with Semicircular Ridge (Fig. 12).—In aracanines and most ostraciines the lateral surface of the hyomandibula is concave and irregular, without definable surface features (0; see Fig. 11; no homologous condition is observed in the other outgroup taxa). In *Lactophrys* species a semicircular ridge is present at the median edge of the preopercular groove (1; this appears to be for insertion of the levator arcus palatini muscle).

37—Rod-like Process of Hyomandibula with Ventral Curvature (Fig. 14).—In the outgroup taxa and most ostraciines the anteriorly directed rod of the hyomandibula is straight (0; see Figs. 11–13). In *Rhynochostracion* species, the anterior rod-like process possesses a distinct ventral curvature (1).

38—Ventral Process on Symplectic (Fig. 13).—In the outgroup taxa and Atlantic ostraciines the symplectic is a roughly triangular bone with a smooth ventral surface (0; tetraodontids show non-homologous modifications). *Lactoria* and *Tetrosomus* species, and *Ostracion cyanurus* and *O. whitleyi* have distinct processes arising from the symplectic at the posterior free surface (1; the remaining Indo-Pacific species examined did not show processes clearly. In some cases this was due to breakage, in others it appears that development may be ontogenetically or environmentally constrained).

Suspensorium: Palato-pterygoid Region

39—Ectopterygoid Laterally Rotated (Fig. 14).—In the outgroup taxa and most ostraciines the ectopterygoid is oriented in the same plane as the remaining bones of the suspensorium (0; see Fig. 13). In *Rhynchostracion* species this bone (and mesopterygoid) is rotated counter-clockwise (1).

The mesopterygoid also undergoes this rotation; this is not considered an independent character.

40—Mesopterygoid Bulge Absent (Fig. 14).—In Aracaninae and most Indo-Pacific ostraciines a distinct bulge is evident on the free posterior surface of the mesopterygoid (0; see Fig. 13; no homologous condition is observed in the other outgroup taxa). In Atlantic ostraciines and *Lactoria fornasini* this bulge is absent (1).

In *Rhynchostracion* species the mesopterygoid is twisted similarly to the ectopterygoid; because of the obvious correlation, this is not treated as an independent character.

Suspensorium: Opercular Region

41—Modifications to Opercle (Figs. 11, 12).—In the outgroup taxa and Indo-Pacific ostraciines the opercle is a roughly triangular bone with a small articulating head for attachment to the ventral surface of the hyomandibula (0). In Atlantic ostraciines the bone and its articulating head have further broadened anteroposteriorly (1). In *Lactophrys* species the blade is expanded anteroventrally to form a distinct, ventrally oriented point (2).

42—Opercle Thin Flattened Shaft (Fig. 13, see also Fig. 14).—In the outgroup taxa and Atlantic ostraciines the opercular blade is relatively broad (0). In all Indo-Pacific ostraciines the blade is reduced in width such that the opercle is little more than an elongate, thin, flattened shaft (1).

In Aracaninae the posterodorsal surface of the operculum bears a distinct, posteriorly oriented process which is lacking in ostraciines. This character might provide additional support for the monophyly of Aracaninae. However, some tetraodontids appear to have a similar process. Additional material will need to be examined before polarity of this character can be determined.

43—Anterior Surface of Subopercle Expanded (Fig. 11).—In the outgroup taxa and Indo-Pacific the subopercle is rounded anteriorly (0; see Figs. 13, 14). In Atlantic ostraciines the anterior surface is expanded anteriorly and slightly ventrally so that a large surface of contact exists between the subopercle and the posteroventral surface of the preopercle (1).

44—Posterior Point of Subopercle Elongate (Fig. 13).—In the outgroup taxa and most ostraciines the subopercle tapers to a point posteriorly (0; see Figs. 11, 12). In *Lactoria fornasini* and *Ostracion cyanurus* the posterior point is elongated (1).

45—Posterior Projection of Preopercle Recurved (Fig. 11, see also Fig. 14).—In the outgroup taxa and most ostraciines the preopercle is slightly expanded in midregion, tapering to straight points anteriorly and posteriorly (0; see Figs. 12, 13). In *Acanthostracion* and *Rhynchostracion* species the posterior projection is recurved (1).

Branchial Apparatus:
Hyoid Arch, Branchiostegal Rays and Urohyal

46—Epihyal Shelf Expanded (Fig. 15).—In the outgroup taxa and Indo-Pacific ostraciines the epihyal has a small, posteriorly oriented shelf which supports the interhyal (0; see Figs. 16, 17). In Atlantic ostraciines the shelf is expanded (1).

47—Joint Ceratohyal/Epihyal Depression (Fig. 16).—In the outgroup taxa, Atlantic ostraciines, and *Lactoria* species a median depression is present in the ceratohyal, close to, but not including the epihyal (0; see Figs. 15, 17). In *Ostra-*

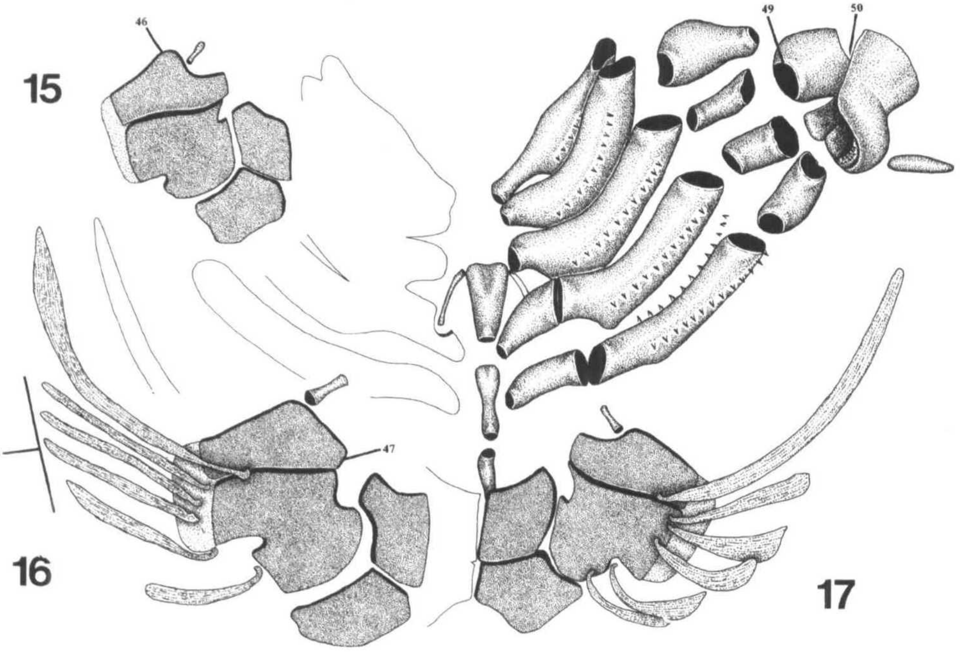

Figure 15. Hyoid arch of *Acanthostracion polygonius*, dorsal view: (46) lateral expansion of epihyal shelf.

Figure 16. Hyoid arch of *Ostracion cubicus*, dorsal view: (47) reduction of epihyal shelf at median contact with ceratohyal; (48) reduction in width of branchiostegal rays.

Figure 17. Branchial apparatus reconstruction based on *Acanthostracion quadricornis*, dorsal view: (49) third pharyngobranchial lacking tooth plate; (50) synchondral joint between pharyngobranchials 2 and 3.

cion species (with the possible exception of *O. cubicus*, for which the data are inconclusive), *Rhynchostracion* and *Tetrosomus* species the anterodorsal surface of the epihyal abutting the pointed edge of the dorsal ceratohyal depression has formed a reduced shelf; associated with this is the reduction of the pointed edge of the ceratohyal such that the epihyal shelf and ceratohyal depression form the same structure (1).

48—Branchiostegal Thickness Reduced (Fig. 16).—In the outgroup taxa and Atlantic ostraciines the branchiostegals are distally expanded (0; see Fig. 17. Tetraodontids exhibit non-homologous modifications). In Indo-Pacific ostraciines they are greatly reduced in width (1).

49—No Teeth on Third Pharyngobranchial (Fig. 17).—In the outgroup taxa three pairs of pharyngobranchials are present, of which the second and third pairs are normally tooth bearing (0). In ostraciines the third is not toothed; it is smaller, columnar, with a concave ventral surface (1).

50—Synchondral Joint between Second and Third Pharyngobranchial (Fig. 17).—In the outgroup taxa and Indo-Pacific ostraciines the second and third pharyngobranchials are separate (0). In Atlantic ostraciines the second and third pharyngobranchials have formed a synchondral joint (1).

51—Tooth Plate on Second Pharyngobranchial Straight.—In Aracaninae and several ostraciines the tooth plate on the second pharyngobranchial is crescent-shaped (0; see Fig. 17; no homologous condition is observed in the other outgroup taxa). In some Indo-Pacific ostraciines—*Rhynchostracion* species, *Ostracion cubicus, O. cyanurus, O. whitleyi,* and *Tetrosomus reipublicae*—the tooth plate on the second pharyngobranchial is not crescent shaped but straight (1; the condition for *Lactoria cornuta* and *L. fornasini* could not be unambiguously identified).

Paired Fin Girdles: Pectoral Fin

52—Baudelot's Ligament.—In Aracaninae both components of Baudelot's ligament are fully ossified and fused both medially and laterally (0?; none of the ostraciines share this state and in balistids, tetraodontoids, and triacanthoids, Baudelot's ligament is both unossified and appears to have different origin and insertion than in ostraciids). In none of the ostraciines is the posteroventral component ossified. The anterodorsal component is fully ossified in aracanines (0), fully ossified but not fused medially in *Acanthostracion* and *Lactophrys* species, and *Lactoria diaphana, Tetrosomus reipublicae,* and *T. concatenatus* (1), partially ossified in *Lactoria cornuta* and *Tetrosomus gibbosus* (2; the condition for *Lactoria fornasini* could not be determined), and completely unossified in *Ostracion* and *Rhynchostracion* species (3).

Because of the inability to polarize these character states unequivocally, I have decided not to include them in the primary analysis. The character is treated as unordered in the database to provide hypotheses of character state evolution based on the other characters.

53—Modification to Dorsal Half of Cleithrum (Fig. 19).—In the outgroup taxa and Atlantic ostraciines the dorsal half of the cleithrum is long and thin, with only a narrow surface of articulation with Baudelot's ligament (0; see Fig. 18). In all Indo-Pacific ostraciines this surface has expanded horizontally (1; the condition for *Ostracion meleagris* was not recovered); in *Ostracion* and *Rhynchostracion* species the dorsal edge has expanded and rounded dorsally (2).

54—Modification to Cleithrum Pyramid (Figs. 18, 20).—In the outgroup taxa, *Ostracion* and *Rhynchostracion* species the pyramid is present merely as an indistinct rounded, narrow thickening associated with a slight indentation on the median surface (0; see Fig. 19); there is no evidence of an associated ventral shelf. In *Lactoria* and *Tetrosomus* species the pyramid is a distinct, narrow-shaped structure with a long median ridge (1). In Atlantic ostraciines the pyramid is much larger with a deeper median indentation. In *Lactophrys* species the pyramid is rounded, without median ridge (2), whereas in *Acanthostracion* species the median ridge is well developed (3).

Because of the inability to polarize these character states unequivocally, I have decided not to include them in the primary analysis. The character is treated as unordered in the database to provide hypotheses of character state evolution based on the other characters.

55—Shelf Evident Ventral to Cleithrum Pyramid (Fig. 20, see also Fig. 18).—In the outgroup taxa and *Ostracion* and *Rhynchostracion* species there is no shelf ventral to the cleithrum pyramid (0; see Fig. 19). In Atlantic ostraciines and *Lactoria* species, the ventral shelf is clearly evident (1).

56—Postcleithra Reduced.—In aracanines and Atlantic ostraciines the postcleithra form a broad but slender plate extending posteriorly along the inner surface of the carapace (0; in all other tetraodontiforms the postcleithra form an elongate,

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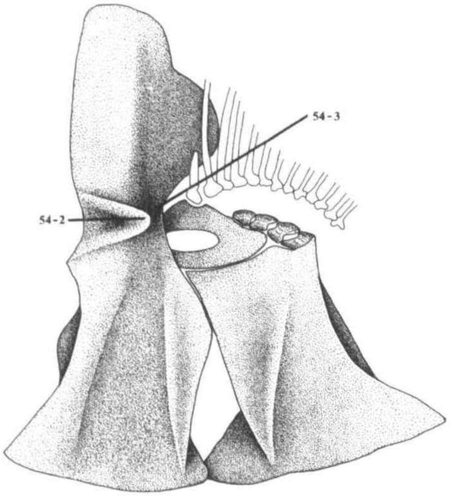

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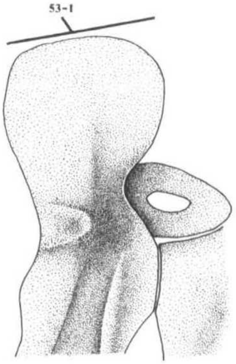

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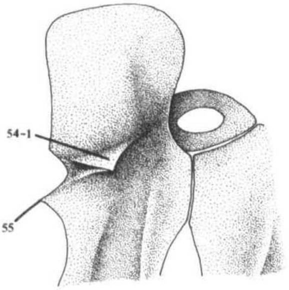


Figure 18. Pectoral girdle of *Acanthostracion polygonius*, lateral view: (54-2) pyramid base broad and rounded; (54-3) broad pyramid with distinct ridge.

Figure 19. Partial cleithrum of *Ostracion cubicus*, lateral view: (53-1) horizontal expansion of dorsal surface.

Figure 20. Partial cleithrum of *Lactoria cornuta*, lateral view: (54-1) pyramid with distinct narrow ridge; (55) shelf ventral to pyramid.

thin blade unlike any ostraciid condition). In Indo-Pacific ostraciines the postcleithra form a thin, short sliver of bone (1).

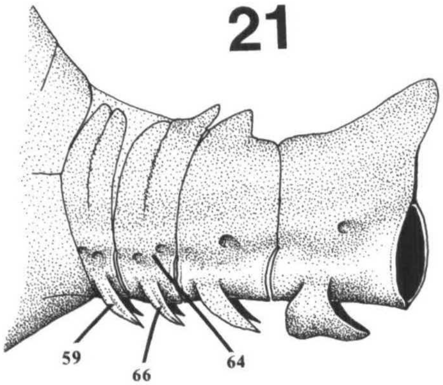
The greatly expanded ventral postcleithrum of aracanines has been interpreted by Winterbottom and Tyler (1983) as an autapomorphy for that group. The relatively reduced elements in Atlantic ostraciines may be intermediate between the aracanine and Indo-Pacific ostraciine condition. If Winterbottom and Tyler's (1983) interpretation of the aracanine condition is correct, then either (or neither) ostraciine condition could be plesiomorphic and any character state polarity decision is equally likely.

57—Posteroventral Edge of Coracoid Rounded.—In the outgroup taxa and most ostraciines the posteroventral edge of the coracoid is pointed (0, see Fig. 18; tetraodontids exhibit non-homologous modifications). In *Lactophrys* species the posteroventral edge is broadly rounded (1).

58—Process on Posterior Edge of Coracoid Absent.—In the outgroup taxa and some Indo-Pacific ostraciines there is a distinct process on the posterior edge of the coracoid, underlying the last actinost (0). This process is absent in *Acanthostracion, Lactophrys,* and *Lactoria* species (1).

Vertebral Column: First Five Abdominal Vertebrae

Maximally, the first five abdominal vertebrae are involved in a fusion complex in ostraciines, these five bones will therefore be considered together. Four com-



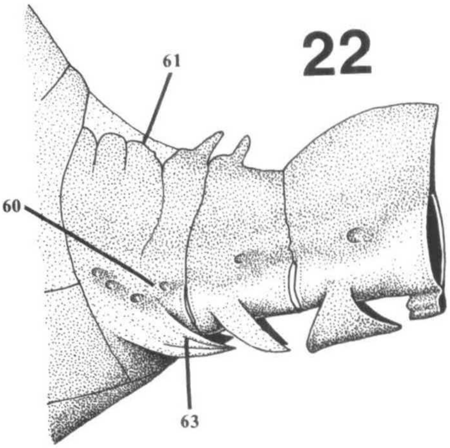


Figure 21 (left). First five vertebrae of *Ostracion meleagris*, lateral view: (59) ventrolateral processes of vertebrae 1 and 2 fused; (64) central of vertebrae 3 and 4 fused; (66) ventrolateral processes of vertebrae 3 and 4 fused.

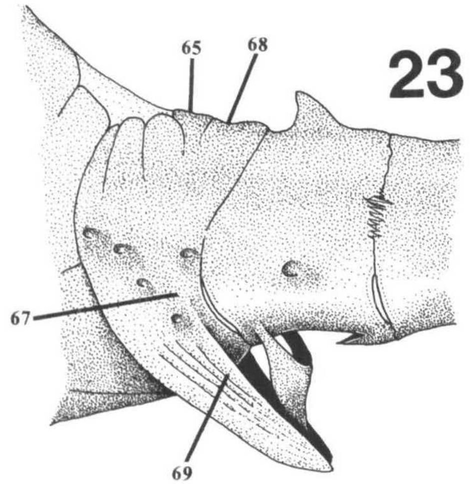
Figure 22 (right). First five vertebrae of *Lactoria cornuta*, lateral view: (60) centra of vertebrae 2 and 3 fused; (61) neural arches of vertebra 3 separated; (63) ventrolateral processes of vertebrae 2 and 3 fused.

ponents of each vertebra have been taken into consideration in character and character state recognition: the centrum, its size and whether it is fused to its anterior neighbor; whether neural arches meet their opposite member dorsally; presence/absence of neural spines; and shape and position of ventrolateral processes. These characters will be discussed for each vertebra separately.

Tyler (1963, 1980) described in some detail the fusion of the first five vertebrae in *Acanthostracion* species. He noted that five neural foramina occur in the upper half of the lateral surface, that separation of neural arches is evident in all but the largest specimens, and that the last three vertebrae possess a very thin centrum and neural arch in single continuous piece separated from those next to it. He also observed for several juvenile specimens that the first two centra fused with one another and with basioccipital, the third and fourth fuse their centra but not with anterior (1 + 2) or posterior (5) centra, even if in large specimens centra of all five anterior vertebrae are fused indistinguishably. It is tempting to assume, a priori, that the fusion of the first five vertebrae is a single transformation series. Considering the outgroup states and the complexity of associated modification (i.e., of the neural arches and spines, and the ventrolateral processes) I considered it more appropriate to assume that each of these characters evolved independently.

In all balistoids the centrum of the first and second abdominal vertebrae is anteroposteriorly compressed. Within Ostraciinae centrum compression is correlated with fusion to the next anterior centrum. In all ostraciids the first two centra are anteriorly fused (the first to the basioccipital at the base of the skull and the second to the first). In all ostraciids the neural arches of the first two vertebrae are dorsally separated; the neural spines of vertebrae 1 and 2 are absent.

59—Ventrolateral Processes of Abdominal Vertebrae 1 and 2 Fused (Fig. 21; see also Figs. 22–24).—In the outgroup taxa the first five abdominal vertebrae bear a pair of pointed, ventrally directed ventrolateral processes; they are not fused to one another (0). All ostraciines have the ventrolateral processes of abdominal vertebrae 1 and 2 fused (1).



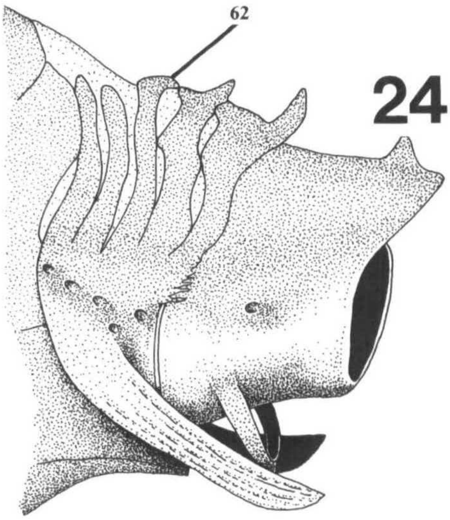


Figure 23 (left). First five vertebrae of *Acanthostracion polygonius*, lateral view: (65) neural spine of vertebra 4 absent; (67) centra of vertebrae 4 and 5 fused; (68) neural spine of vertebra 5 absent; (69) ventrolateral processes of vertebrae 4 and 5 fused.

Figure 24 (right). First five vertebrae of *Lactophrys trigonus*, lateral view: (62) neural spine of abdominal vertebra 3 absent.

60—Centra of Abdominal Vertebrae 2 and 3 Fused (Fig. 22; see also Figs. 23, 24).—In the outgroup taxa and *Ostracion* and *Rhynchostracion* species the centra of abdominal vertebrae 2 and 3 are not fused (0; see Fig. 21). In Atlantic ostraciines, and *Lactoria* and *Tetrosomus* species the centra of abdominal vertebrae 2 and 3 are fused to one another (1).

61—Neural Arches of Abdominal Vertebra 3 Not Joined (Fig. 22; see also Figs. 21, 23).—In the outgroup taxa and *Lactophrys* species the neural arches of abdominal vertebra 3 are joined dorsally to their opposite member (0; Fig. 24). In *Acanthostracion* species and Indo-Pacific ostraciines the neural arches of vertebra 3 are separated (1).

62—Neural Spine of Abdominal Vertebra 3 Absent (Fig. 24; see also Figs. 21–23).—In the outgroup taxa abdominal vertebra 3 bears a neural spine (0). In all ostraciines the neural spine of vertebra 3 is absent (1).

63—Ventrolateral Processes of Abdominal Vertebrae 2 and 3 Fused (Fig. 22; see also Figs. 23, 24).—In the outgroup taxa and *Ostracion* and *Rhynochostracion* species the ventrolateral processes of abdominal vertebrae 2 and 3 are not fused (0; see Fig. 21). In Atlantic ostraciines and *Lactoria* and *Tetrosomus* species the ventrolateral processes of abdominal vertebrae 2 and 3 are fused to one another (1).

64—Centra of Abdominal Vertebrae 3 and 4 Fused (Fig. 21; see also Figs. 22–24).—In the outgroup taxa the centra of abdominal vertebrae 3 and 4 are not fused (0). In all ostraciines the centra of abdominal vertebrae 3 and 4 are fused to one another (1).

65—Neural Spine of Abdominal Vertebra 4 Absent (Fig. 23).—In the outgroup taxa and most ostraciines abdominal vertebra 4 bears a neural spine (0; see Figs. 21, 22, 24). In *Acanthostracion* species the neural spine of vertebra 4 is absent (1).

66—Ventrolateral Processes of Abdominal Vertebrae 3 and 4 Fused (Fig. 21; see also Figs. 22–24).—In the outgroup taxa the ventrolateral processes of abdominal vertebrae 3 and 4 are not fused. In all ostraciines the ventrolateral processes of abdominal vertebrae 3 and 4 are fused to one another (1).

67—Centra of Abdominal Vertebrae 4 and 5 Fused (Fig. 23; see also Fig. 24).—In the outgroup taxa and Indo-Pacific ostraciines the centra of abdominal vertebrae 4 and 5 are not fused (0; see Figs. 21, 22). In Atlantic ostraciines the centra of abdominal vertebrae 4 and 5 are fused to one another (1).

68—Neural Spine of Abdominal Vertebra 5 Absent (Fig. 23).—In the outgroup taxa and most ostraciines abdominal vertebra 5 bears a neural spine (0; see Figs. 21, 22, 24). In *Acanthostracion polygonius* and *A. quadricornis* the neural spine of vertebra 5 is absent (1).

69—Ventrolateral Processes of Abdominal Vertebrae 4 and 5 Fused (Fig. 23; see also Fig. 24).—In the outgroup taxa and Indo-Pacific ostraciines the ventrolateral processes of abdominal vertebrae 4 and 5 are not fused (0; see Figs. 21, 22). In Atlantic ostraciines the ventrolateral processes of abdominal vertebrae 4 and 5 are fused to one another (1).

Vertebral Column: Caudal Vertebrae

The first caudal vertebra is defined as being the first vertebra the ventral surface of which is articulated to the distal tip of the first anal basal pterygiophore (see section on anal basal pterygiophores for more detail). First and second caudal vertebrae similar to eighth and ninth abdominal, centra not fused. Bases of neural arches sutured to those of neighbors, neural spines well developed although slightly smaller than preceding; ventrolateral processes reduced.

70—Neural Spine of Caudal Vertebra 3 Reduced (Fig. 31).—In the outgroup taxa and most ostraciines caudal vertebra 3 bears a neural spine (0; see Figs. 25, 26). In *Lactoria fornasini* and *Tetrosomus* species the neural spine is either reduced (1; *L. fornasini*) or absent (2; the latter species).

71—Small Triangular Dorsolateral Process on Caudal Vertebra 3 (Fig. 30; see also Figs. 28, 29).—In balistids, aracanines and most ostraciines caudal vertebra 3 lacks dorsolateral processes (0; see Figs. 25–27). *Lactoria diaphana, Ostracion* and *Rhynchostracion* species possess a small triangular dorsolateral process (1).

A similar process is also observed in tetraodontids, they are therefore coded as having the derived state. It is questionable that the presence of such a process in these taxa is homologous, the question does, however, bear further investigation.

72—Neural Spine of Caudal Vertebra 4 Reduced (Fig. 31).—In the outgroup taxa and most ostraciines caudal vertebra 4 bears a neural spine (0; see Figs. 25, 26). In *Lactoria fornasini* and *Tetrosomus* species the neural spine of vertebra 4 is either reduced (1; *L. fornasini*) or absent (2; the latter species).

73—Enlarged Dorsolateral Process on Caudal Vertebra 4 (Fig. 30; see also Figs. 28, 29).—In balistids, aracanines and most ostraciines caudal vertebra 4 lacks dorsolateral processes (0; see Figs. 25–27). *Lactoria diaphana, Ostracion* and *Rhynchostracion* species possess an enlarged dorsolateral process (1).

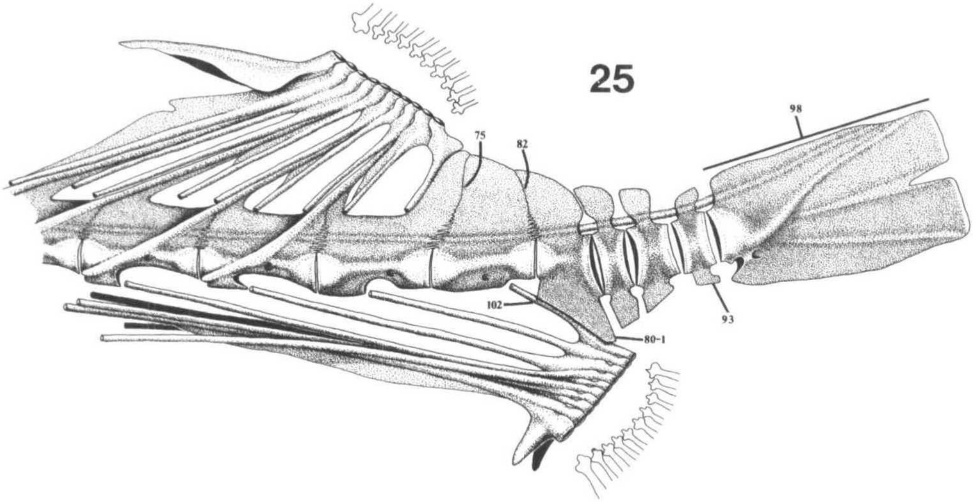
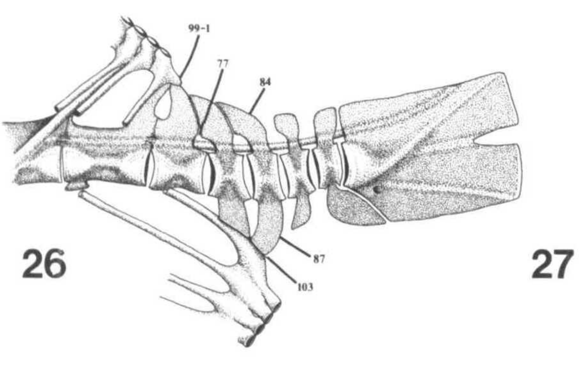


Figure 25. Caudal skeleton reconstruction for *Acanthostracion polygonius*, lateral view: (75) neural spines of caudal vertebrae 3 and 4 fused; (80-1) haemal spine with lateral projections and median groove; (82) neural spines of caudal vertebrae 4 and 5 fused; (93) haemal spine of caudal vertebra 8 fused to haemal arches; (98) centrum-hypural plate elongate; (102) shaft of last anal basal pterygiophore joined to haemal spine of caudal vertebra 5.

A similar process is also observed in tetraodontids, they are therefore coded as having the derived state. It is questionable that the presence of such a process in these taxa is homologous, the question does, however, bear further investigation.

74—Short Broad Pair of Ventrolateral Processes on Caudal Vertebra 4 (Fig. 29; see also Figs. 28, 30).—In the outgroup taxa and most ostraciines caudal vertebra 4 lacks ventrolateral processes (0; see Figs. 25–27, 31). *Lactoria diaphana, Ostracion* and *Rhynchostracion* species possess a pair of short, broad ventrolateral processes which articulate with the ossified flange of the last anal basal pterygiophore (1).



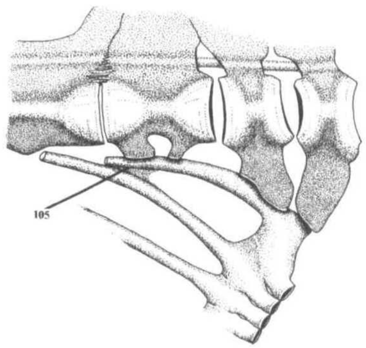
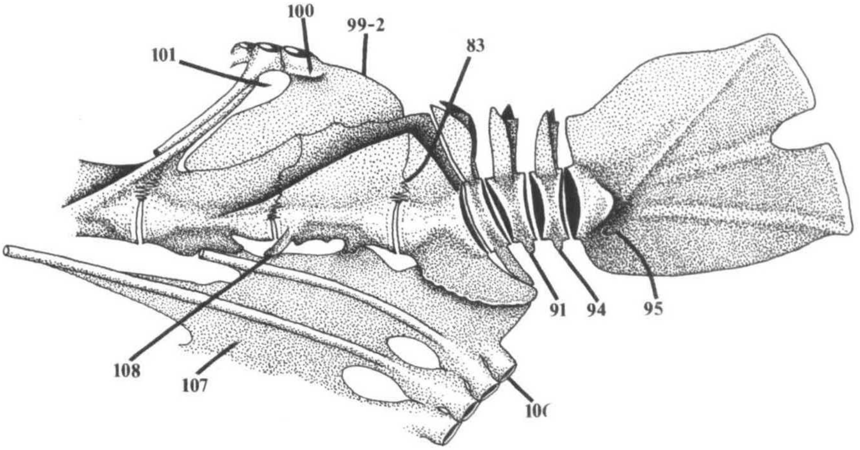


Figure 26 (left). Partial caudal skeleton of *Lactophrys bicaudalis*, lateral view: (77) neural arch base of caudal vertebrae 4 and 5 not sutured; (84) neural spine of vertebra 6 enlarged; (87) haemal spine of vertebra 6 enlarged; (99-1) last dorsal pterygiophore overlies neural spine of caudal vertebra 4; (103) last anal basal pterygiophore joined to haemal spine of caudal vertebra 6.

Figure 27 (right). Partial caudal skeleton of *Lactophrys triqueter*, lateral view: (105) shafts of last and second last anal basal pterygiophores partly joined.



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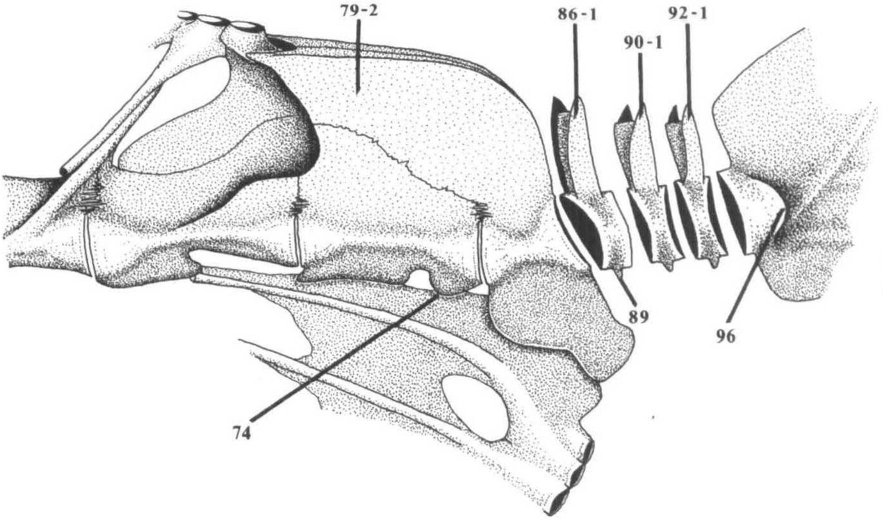

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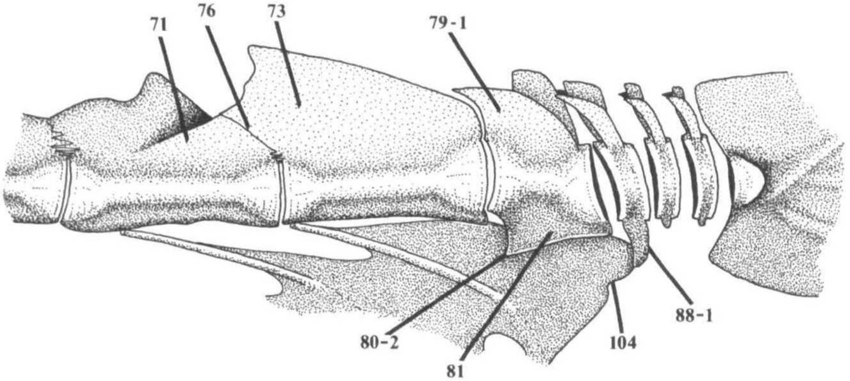
Figure 28 (upper). Partial caudal skeleton of *Ostracion meleagris*, lateral view: (83) dorsolateral processes of vertebrae 4 and 5 joined; (91) reduced haemal spine of caudal vertebra 7; (94) reduced haemal spine of caudal vertebra 8; (95) haemal foramen of centrum-hypural plate reduced; (99-2) last dorsal pterygiophore overlies neural spine of caudal vertebra 5; (100) lateral expansion on last dorsal basal pterygiophore; (101) penultimate dorsal basal pterygiophore absent; (106) shaft of last anal basal pterygiophore absent; (107) gaps between pterygiophores mostly filled; (108) shaft of penultimate anal basal pterygiophore partially joined to ventral surface of caudal vertebra 4.

Figure 29 (lower). Partial caudal skeleton of *Ostracion nasus*, lateral view: (74) small ventrolateral process on caudal vertebra 4; (79-2) large, triangular dorsolateral process on caudal vertebra 5 expanded and joined dorsally; (86-1) pair of autogenous dorsolateral processes on vertebra 6; (89) haemal spine of caudal vertebra 6 reduced; (90-1) pair of autogenous dorsolateral processes on vertebra 7; (92-1) pair of autogenous dorsolateral processes on vertebra 8; (96) vertical ridge on centrum-hypural plate.

75—Neural Spines of Caudal Vertebrae 3 and 4 Joined (Fig. 25; see also Figs. 26, 28).—In the outgroup taxa and *Lactoria* and *Tetrosomus* species neural spines of caudal vertebrae 3 and 4 are not joined (0). In Atlantic ostraciines and *Ostracion* and *Rhynchostracion* species the neural spines of caudal vertebrae 3 and 4 are joined/fused to one another (1).



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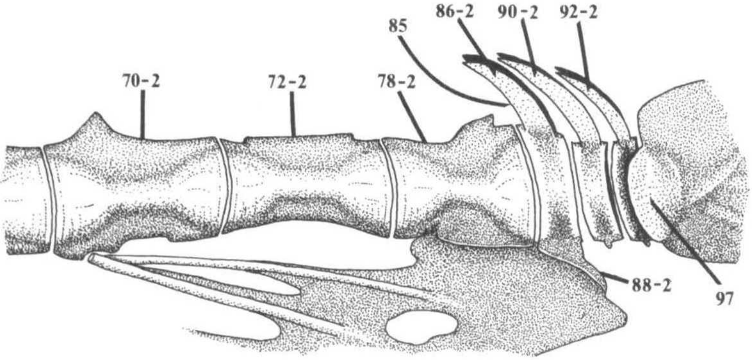

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Figure 30 (upper). Partial caudal skeleton of *Lactoria diaphana*, lateral view: (71) small, triangular dorsolateral process on caudal vertebra 3; (73) large, triangular dorsolateral process on caudal vertebra 4; (76) dorsolateral processes of vertebrae 3 and 4 joined; (79-1) large, triangular dorsolateral process on caudal vertebra 5; (80-2) haemal spine of caudal vertebra 5 with lateral projections extending over surface of anal basal pterygiophores; (81) ventral extent of haemal spine of caudal vertebra 5 reduced; (88-1) haemal spine of caudal vertebra 6 with lateral projections joined to base of last anal basal pterygiophore; (104) base of last anal basal pterygiophore posterodorsally expanded.

Figure 31 (lower). Partial caudal skeleton of *Lactoria gibbosus*, lateral view: (70-2) neural spine of caudal vertebra 3 absent; (72-2) neural spine of caudal vertebra 4 absent; (78-2) neural spine of caudal vertebra 5 absent; (85) neural spine of caudal vertebra 6 reduced; (86-2) dorsolateral processes of caudal vertebra 6 enlarged and angled forward; (88-2) haemal spine of caudal vertebra 6 with lateral projections extending beyond and joining posterior to pterygiophore base; (90-2) dorsolateral processes of caudal vertebra 7 enlarged and angled forward; (92-2) dorsolateral processes of caudal vertebra 8 enlarged and angled forward; (97) anterolateral margins of centrum-hypural plate enlarged anteriorly.

76—Dorsolateral Processes of Caudal Vertebrae 3 and 4 Joined (Fig. 30; see also Figs. 28, 29).—In the outgroup taxa and most ostraciines dorsolateral processes on caudal vertebrae 3 and 4 (if present) are not joined (0). In *Ostracion* and *Rhynchostracion* species, and *Lactoria diaphana* the dorsolateral processes of caudal vertebrae 3 and 4 are joined to one another (1).

77—Neural Arch Bases of Caudal Vertebrae 4 and 5 Not Fused (Fig. 26).—In aracanines and most ostraciines the neural arch bases of caudal vertebrae 4 and 5 are fused (0; see Fig. 25; the amount of vertebral fusion observed in ostraciids is non-homologous with the other outgroup taxa). In *Lactophrys* species the neural arch bases of caudal vertebrae 4 and 5 are not fused to one another (1).

78—Neural Spine of Caudal Vertebra 5 Reduced (Fig. 31).—In the outgroup taxa and most ostraciines caudal vertebra 5 bears a neural spine (0; see Figs. 25, 26, 28, 30). In *Lactoria fornasini* and *Tetrosomus* species the neural spine of vertebra 5 is either reduced (1; *L. fornasini*) or absent (2; the latter species).

79—Caudal Vertebra 5 with Dorsolateral Processes (Figs. 29, 30; see also Fig. 28).—In balistids, aracanines and many ostraciines caudal vertebra 5 lacks dorsolateral processes (0; see Figs. 25, 26, 31). In *Ostracion, Rhynchostracion,* and *Lactoria* species vertebra 5 possesses a pair of dorsolateral processes (1; due to overall reduction of vertebral elements in *Tetrosomus* species, character state is coded as equivocal); in *Rhynchostracion nasus* and *R. rhinorhynchus* these processes are greatly enlarged and dorsally joined (2).

A similar process is also observed in tetraodontids, they are therefore coded as having the derived state. It is questionable that the presence of such a process in these taxa is homologous, the question does, however, bear further investigation.

80—Modifications to Haemal Spine of Caudal Vertebra 5 (Figs. 25, 30).—In balistids and aracanines the haemal spine abuts to but does not fuse with the shaft of the last anal basal pterygiophore (0; this condition is non-homologous with that in tetraodontids). In all ostraciines the haemal spine has formed lateral projections and a median groove joining it to the pterygiophore (1). In *Lactoria* and *Tetrosomus* species the lateral projections from the haemal spine largely overlap the base of the last anal basal pterygiophore (2).

81—Size of Haemal Spine of Caudal Vertebra 5 Reduced (Fig. 30; see also Fig. 31).—In balistids, aracanins and most ostraciines the haemal spine is large and broad (0; see Fig. 25; this condition is non-homologous with that in tetraodontids). In *Lactoria* and *Tetrosomus* species the ventral extent of the haemal spine is greatly reduced (1).

82—Neural Spines of Caudal Vertebrae 4 and 5 Joined (Fig. 25).—In the outgroup taxa and *Lactoria* and *Tetrosomus* species the neural spines of caudal vertebrae 4 and 5 are not joined (0). In *Acanthostracion, Lactophrys,* and *Ostracion* species the neural spines of caudal vertebrae 4 and 5 are joined to one another (1; I could not identify this condition for *Rhynchostracion* species).

83—Dorsolateral Processes of Caudal Vertebrae 4 and 5 Joined (Fig. 28).—In the outgroup taxa and most ostraciines the dorsolateral processes of caudal vertebrae 4 and 5 (if present) are not joined (0; see Fig. 30). In *Ostracion* and *Rhynchostracion* species the dorsolateral processes of caudal vertebrae 4 and 5 are joined to one another (1; better developed in *Rhynchostracion* species, which is why I could not identify the condition for previous character).

84—Neural Spine of Caudal Vertebra 6 Enlarged (Fig. 26).—In the outgroup taxa and most ostraciines the neural spine of caudal vertebra 6 is smaller than that of vertebra 5 (0; see Fig. 25). In *Lactophrys* species the neural spine of vertebra 6 is enlarged with the distal end angled anteriorly (1).

85—Neural Spine of Caudal Vertebra 6 Reduced (Fig. 31).—In the outgroup taxa and most ostraciines the neural spine of caudal vertebra 6 is smaller than that of vertebra 5 (0; see Fig. 25). In *Tetrosomus* species the neural spine is further reduced (1).

86—Caudal Vertebra 5 with Dorsolateral Processes (Fig. 29, 31; see also Figs. 28, 30).—In balistids, aracanines and Atlantic ostraciines caudal vertebra 5 lacks dorsolateral processes (0; see Figs. 25, 26). In Indo-Pacific ostraciines caudal vertebra 6 bears dorsolateral processes (1); these are greatly enlarged and angle anteriorly in *Lactoria* and *Tetrosomus* species (2).

A similar process is also observed in tetraodontids; they are therefore coded as having the derived state. It is questionable that the presence of such a process in these taxa is homologous, the question does, however, bear further investigation.

87—Haemal Spine of Caudal Vertebra 6 Enlarged (Fig. 26).—In the outgroup taxa and most ostraciines the haemal spine of caudal vertebra 6 is reduced relative to that of vertebra 5 (0; see Fig. 25). In *Lactophrys* species the haemal spine is enlarged with the distal end angled anteriorly (1).

88—Modifications to Haemal Spine of Caudal Vertebra 6 (Figs. 30, 31).—In the outgroup taxa and most ingroup taxa the haemal spine of caudal vertebra 6 makes no contact with anal basal pterygiophores (0; see Fig. 25). In *Lactoria* and *Tetrosomus* species a pair of ventrolateral processes is present which join to the base of the last anal basal pterygiophore (1); in all these species except *Lactoria diaphana* these processes join posteriorly around the pterygiophore base (2).

89—Reduced Haemal Spine on Caudal Vertebra 6 (Fig. 29).—In the outgroup taxa and most ostraciines the haemal spine of caudal vertebra 6 is reduced relative to that of vertebra 5 but still distinct (0; see Fig. 25). In *Ostracion* and *Rhynchostracion* species (except *O. meleagris*) the haemal spine is further reduced (1).

90—Caudal Vertebra 7 with Dorsolateral Processes (Figs. 29, 31; see also Figs. 28, 30).—In balistids, aracanines and Atlantic ostraciines caudal vertebra 7 lacks dorsolateral processes (0; see Fig. 25). In all Indo-Pacific ostraciines it bears a pair of dorsolateral processes (1); these are greatly enlarged and angle anteriorly in *Tetrosomus* species (2).

A similar process is also observed in tetraodontids, they are therefore coded as having the derived state. It is questionable that the presence of such a process in these taxa is homologous, the question does, however, bear further investigation.

91—Reduced Haemal Spine of Caudal Vertebra 7 (Fig. 28; see also Figs. 29–31).—In the outgroup taxa and most Atlantic ostraciines the haemal spine of caudal vertebra 7 is reduced but still distinct (0; see Fig. 25). In *Lactophrys trigonus* and all Indo-Pacific ostraciines the haemal spine is further reduced (1).

92—Caudal Vertebra 8 with Dorsolateral Processes (Figs. 29, 31; see also Figs. 28, 30).—In balistids, aracanines and Atlantic ostraciines caudal vertebra 7 lacks dorsolateral processes (0; see Fig. 25). In all Indo-Pacific ostraciines it bears a pair of dorsolateral processes (1); these are greatly enlarged and angle anteriorly in *Tetrosomus* species (2).

A similar process is also observed in tetraodontids, they are therefore coded as having the derived state. It is questionable that the presence of such a process in these taxa is homologous, the question does, however, bear further investigation.

93—Haemal Spine of Caudal Vertebra 8 Fused to Haemal Arches (Fig. 25).—In the outgroup taxa and *Lactophrys* species the haemal spine of caudal vertebra 8 is joined synchondrally to the ventral surface of the centrum (0; see Fig. 26). In *Acanthostracion* species and Indo-Pacific ostraciines this spine is fused to the haemal arches (1).

94—Haemal Spine of Caudal Vertebra 8 Reduced (Fig. 28; see also Figs. 29–31).—In the outgroup taxa and Atlantic ostraciines the haemal spine of caudal vertebra 8 is distinct (0; see Figs. 25, 26). In Indo-Pacific ostraciines it is much reduced (1).

Vertebral Column: Centrum-hypural Plate

95—Haemal Canal Foramen on Centrum-hypural Plate Reduced (Fig. 28).—In aracanines and Atlantic ostraciines the foramen marking the anteroventral junction between parhypural and hypurals is large and distinct (0; see Figs. 25, 26; tetraodontids and balistids have non-homologous plate morphology). In Indo-Pacific ostraciines the foramen is reduced to absent (1).

96—Vertical Ridge on Anterolateral Surface of Centrum-hypural Plate (Fig. 29, see also Figs. 28, 30).—In the outgroup taxa and most ostraciines the anterolateral surface of the centrum-hypural plate is smoothly rounded (0; see Figs. 25, 26). In *Lactoria diaphana, L. fornasini* and *Ostracion* and *Rhynchostracion* species there is a vertical ridge on the lateral surface of the centrum-hypural plate at the level of fusion between last vertebra and rest of the plate (1).

97—Anterolateral Margin of Centrum-hypural Plate Anteriorly Expanded (Fig. 31).—In the outgroup taxa and most ostraciines the anterior margin of the centrum-hypural plate is no different than the centrum margins of the preceding caudal vertebrae (0; see Figs. 25, 26, 28–30). In *Tetrosomus* species the anterolateral margins of the centrum-hypural plate are anteriorly expanded to partially cover the centrum of the penultimate (#8) caudal vertebra (1).

98—Centrum-hypural Plate Posteriorly Expanded (Fig. 25; see also Fig. 26).—In the outgroup taxa and Indo-Pacific ostraciines the centrum-hypural plate is short and stout (0; see Fig. 28). In Atlantic ostraciines the plate is posteriorly elongated (1).

Dorsal and Anal Fins

99—Extent of Posterior Expansion of Last Dorsal Basal Pterygiophore (Figs. 26, 28).—In the outgroup taxa and *Acanthostracion* species the posterior margin of the last dorsal basal pterygiophore is maximally expanded to the anterodorsal margin of the neural spine of caudal vertebra 3 (0; see Fig. 25). In *Lactophrys* species the posteroventral edge of the last pterygiophore is posteriorly expanded to overlie anterior surface of neural spine of caudal vertebra 4 (1); in *Ostracion* and *Rhynchostracion* species the posterior expansion includes the neural spine of caudal vertebra 5 (2; due to the reduction of the dorsal elements of the caudal vertebrae in *Lactoria* and *Tetrosomus* species, it was not possible to determine state distribution for this character).

100—Lateral Expansion on Posterior Part of Last Dorsal Basal Pterygiophore (Fig. 28; see also Fig. 29).—In the outgroup taxa and Atlantic ostraciines the last dorsal basal pterygiophore lacks any lateral expansions (0; see Fig. 25). In Indo-Pacific ostraciines there is a lateral expansion on the posterior part of the last dorsal basal pterygiophore (1).

101—Penultimate Dorsal Basal Pterygiophore Absent (Fig. 28; see also Fig. 29).—In the outgroup taxa and Atlantic ostraciines there are usually 10 pterygiophores (including Tyler's (1980) supraneural), with the last two situated between the neural spines of caudal vertebrae 2 and 3 (0; see Fig. 25). In Indo-Pacific ostraciines the penultimate pterygiophore is absent (1).

102—Base of Last Anal Basal Pterygiophore Fused to Distal End of the Haemal Spine of Caudal Vertebra 5 (Fig. 25).—In the outgroup taxa the anal basal pterygiophores are often associated with the bases of one or more caudal vertebrae but never fused to them (0). In all ostraciines the base of the last anal basal pterygiophore fuses to the distal end of the haemal spine of caudal vertebra 5 (1).

103—Base of Last Anal Basal Pterygiophore Joined to Expanded Haemal Spine of Caudal Vertebra 6 (Fig. 26; see also Fig. 27).—In the outgroup taxa and most ostraciines the base of the last anal basal pterygiophore is not joined to the haemal spine of caudal vertebra 6 (0; see Fig. 25). In *Lactophrys* species the base of the last anal basal pterygiophore is also joined to the anteroventrally-expanded tip of the haemal spine of vertebra 6 (1; note similar but non-homologous Char. 88).

104—Base of Last Anal Basal Pterygiophore Expanded Dorsally (Fig. 30).—In the outgroup taxa and most ostraciines the base of the last anal basal pterygiophore is not dorsally expanded (0; see Fig. 25). In *Lactoria* and *Tetrosomus* species the base is posterodorsally expanded and joined to the groove provided by the ventrolateral processes (1).

105—Ultimate and Penultimate Anal Basal Pterygiophores at Least Partially Fused along Their Lengths (Fig. 27).—In the outgroup taxa and most ostraciines the ultimate and penultimate anal basal pterygiophores are distinct (0; see Fig. 25). In *Lactophrys triqueter* and *L. trigonus* the last and second last pterygiophores are fused at least partially along their lengths (1).

106—Ultimate Anal Basal Pterygiophore Absent (Fig. 28; see also Fig. 29).—In balistids, aracanines and most ostraciines the ultimate anal basal pterygiophore is present (i.e., can be traced to the distal cup-like base) (0; see Figs. 25–27; tetraodontids have non-homologous modifications). In Indo-Pacific ostraciines the shaft of the last anal basal pterygiophore is absent, though the distal cup remains (1).

107—Posterior Anal Basal Pterygiophores Connected by Ossified Flanges (Fig. 28; see also Figs. 29–31).—In the outgroup taxa and Atlantic ostraciines the shafts of the posterior three anal basal pterygiophores are distinct (note Char. 105) (0; see Figs. 25, 26). In Indo-Pacific ostraciines these pterygiophores are connected to one another via median ossified flanges similar to the one on the anteroventral surface of anal basal pterygiophore 1 (1).

108—Ossified Flange of Last Anal Basal Pterygiophore Joined to Ventral Surface of Caudal Vertebra 4 (Fig. 28; see also Figs. 29, 30).—In the outgroup taxa and most ostraciines no median ossified flange exists to connect the last anal basal pterygiophore to caudal vertebra 4 (0; see Figs. 25, 26). In *Ostracion* and *Rhynchostracion* species and *Lactoria diaphana* an ossified flange exists which connects the last anal basal pterygiophore to the ventral surface of caudal vertebra 4 (1).

(3) Phylogeny

Characters Not Used.—Of the 139 potential osteological characters examined for the phylogenetic analysis, 31 were found to be unusable (Table 1). These can be grouped into two categories: those that are invariant in the ingroup (and therefore not even potentially useful), and those for which some variation was observed (thus having some potential if future examinations show the present interpretation to have been inaccurate). Among the latter, variation was either found to be insufficient to confidently identify character states, or too variable within species, rendering them polymorphic, or both.

Bones/bone groups with invariant characters were: basioccipital, vomer, quadrate, metapterygoid, palatine, angulo-articular, retroarticular, hypohyals, inter-

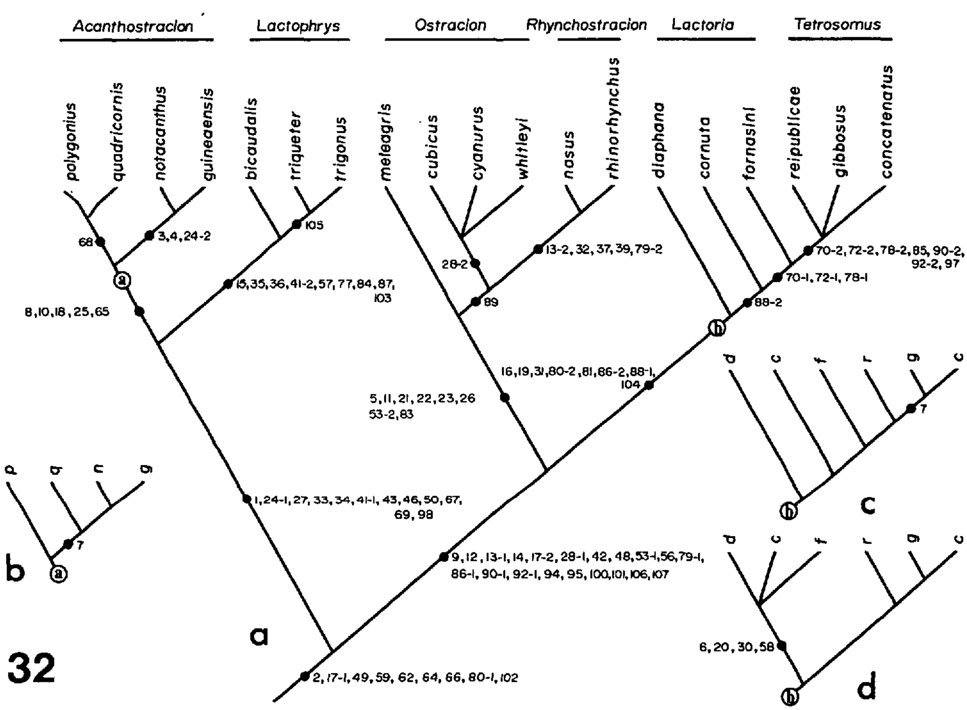

Figure 32. Phylogeny reconstruction for the 19 Ostraciinae species studied. (a) topology reconstruction based on synapomorphic character states only. Numbers at nodes represent character states as described in the results section. (b, c, d) alternate topologies at nodes 'a' and 'b' based on homoplastic resolution. Recognition of *Rhynchostracion* and *Tetrosomus* would render *Ostracion* and *Lactoria*, respectively, paraphyletic.

hyals, urohyal, basibranchials, ceratobranchials, epibranchials, posttemporal, supracleithrum, actinosts, fin rays, abdominal vertebra 1, caudal vertebra 1, caudal vertebra 2.

Bones/bone groups with unpredictably variable characters were: interopercle, premaxilla, maxilla, dentary, ceratohyals, hypobranchials, scapula, abdominal vertebra 6, abdominal vertebra 7, abdominal vertebra 8, abdominal vertebra 9.

Genus and Species Level Relationships.—The computer-generated analysis resulted in two equally parsimonious cladograms 158 steps long, a consistency index (c.i.) of 80% and a retention index (r.i.) of 94% (Fig. 32a − below node 'b' − plus Figs. 32b+c and 32c − above node 'b' −, respectively). The two unordered characters were included in this calculation; if they are excluded, the cladograms are 151 steps long with a c.i. of 80% and identical topologies. Both computer-generated cladograms differed from the hand-generated one (Fig. 32a) in resolving the trichotomy involving *Tetrosomus reipublicae, Tetrosomus gibbosus,* and *T. concatenatus* (Fig. 32c). In addition, one of the cladograms differed in its resolution of relationships among *Acanthostracion* species. Instead of being the sister species to *A. quadricornis, A. polygonius* was hypothesized to be the sister to all other *Acanthostracion* species (Fig. 32b). Both of these differences are attributed to the single homoplastic character 7 (expansion of the sphenotic ridge to form a broad shelf).

According to the cladistic analysis two genus level problems are evident (Fig.

32). Continued recognition of *Rhynchostracion* and *Tetrosomus* would result in rendering *Ostracion* and *Lactoria,* respectively, paraphyletic. I propose, therefore, that (a) *Rhynchostracion* be considered a junior synonym of *Ostracion* (with *O. nasus* and *O. rhinorhynchus*), (b) *Tetrosomus* be considered a junior synonym of *Lactoria* (with *L. reipublicae, L. gibbosus,* and *L. concatenatus*).

Synapomorphy Scheme (Fig. 32a).—In addition to the 16 myological characters and 20 osteological characters reported by Winterbottom and Tyler (1983; see character descriptions for comments), 9 synapomorphic character states are recognized for all ostraciines: 2 (supraoccipital crest absent); 17-1 (frontal contacts ethmoid cartilage); 49 (no teeth on third pharyngobranchial); 59 (ventrolateral processes of abdominal vertebrae 1 and 2 fused); 62 (neural spine of abdominal vertebra 3 absent); 64 (centrum of abdominal vertebrae 3 and 4 fused); 66 (ventrolateral processes of abdominal vertebrae 3 and 4 fused); 80-1 (haemal spine of caudal vertebra 5 fused to base of last anal basal pterygiophore); 102 (base of last anal basal pterygiophore fuses to distal end of the haemal spine of caudal vertebra 5).

Synapomorphic for all Atlantic ostraciines are 12 character states: 1 (exoccipitals dorsally separated by cartilage); 24-1 (parasphenoid/vomer contact posteriorly convex); 27 (anterior projections of pterosphenoids elongated and fused); 33 (space separating opercular process from preopercular groove on hyomandibula); 34 (hyomandibula with posteroventral process); 41-1 (articulating head of opercle very wide); 43 (anterior surface of subopercle expanded); 46 (epihyal shelf expanded); 50 (synchondral joint between second and third pharyngobranchial); 67 (centra of abdominal vertebrae 4 and 5 fused); 69 (ventrolateral processes of abdominal vertebrae 4 and 5 fused); 98 (centrum-hypural plate posteriorly expanded).

Synapomorphic for *Acanthostracion* species are five character states: 8 (sphenotic forms ventral extension of orbital ridge); 10 (absence of epiotic crest); 18 (lateral ethmoid ridge narrow along entire length); 25 (parasphenoid with symmetrical lateral ridges); 65 (neural spine of abdominal vertebra 4 absent).

Synapomorphic for *A. polygonius* and *A. quadricornis* is 68 (neural spine of abdominal vertebra 5 absent).

Synapomorphic for *A. notacanthus* and *A. guineaensis* are three character states: 3 (anterior margin of supraoccipital lacking triangular wedge); 4 (posterior margin of supraoccipital with triangular wedge between exoccipitals); 24-2 (joint between parasphenoid and vomer medially pointed).

Synapomorphic for *Lactophrys* species are nine character states: 15 (large gap between prootic shelf and parasphenoid); 35 (hyomandibula dorsoventrally flattened); 36 (hyomandibula with semicircular ridge); 41-2 (opercular blade anteroventrally expanded); 57 (posteroventral edge of coracoid rounded); 77 (neural arch bases of caudal vertebrae 4 and 5 not fused); 84 (neural spine of caudal vertebra 6 enlarged); 87 (haemal spine of caudal vertebra 6 enlarged); 103 (base of last anal basal pterygiophore joined to expanded haemal spine of caudal vertebra 6).

Synapomorphic for *L. triqueter* and *L. trigonus* is 105 (last and second last anal basal pterygiophores at least partially fused along their lengths).

Synapomorphic for all Indo-Pacific ostraciines are 21 character states: 9 (sphenotic expanded dorsally); 12 (posterior surface of prootic expanded anteriorly); 13-1 (suborbital shelf of prootic angled at 30–40 degrees from horizontal); 14 (ventral keel of suborbital shelf reduced); 17-2 (anterior edge of frontal contact lateral ethmoids); 28-1 (anterior projection of pterosphenoid reduced); 38 (ventral process on symplectic); 42 (opercle thin, flattened shaft); 48 (branchiostegal thickness reduced); 53-1 (dorsal half of cleithrum expanded horizontally); 56 (postcleithra reduced); 79-1 (cauda vertebra 5 with dorsolateral processes); 86-1 (caudal vertebra 6 with dorsolateral processes); 90-1 (caudal vertebra 7 with dorsolateral processes); 92-1 (caudal vertebra 8 with dorsolateral processes); 94 (haemal spine of caudal vertebra 8 reduced); 95 (haemal canal foramen on centrum-hypural plate reduced); 100 (lateral expansion on posterior part of last dorsal basal pterygiophore); 101 (penultimate dorsal basal pterygiophore absent); 106 (ultimate anal basal pterygiophore absent); 107 (posterior anal basal pterygiophores connected by ossified flanges).

Synapomorphic for *Ostracion* species are eight character states: 5 (pterotic shaft expanded laterally); 11 (epiotic crest horizontal); 21 (lateral ethmoids dorsoventrally flattened); 22 (median surface of lateral ethmoids convex); 23 (posterolateral flange on distal tip of lateral ethmoids); 26 (dorsal midorbital keel of parasphenoid reduced); 53-2 (expanded dorsal half of cleithrum dorsally rounded); 83 (dorsolateral processes of caudal vertebrae 4 and 5 joined).

Synapomorphic for *O. cubicus, O. cyanurus, O. whitleyi, O. nasus* and *O. rhinorhynchus* is character state 89 (reduced haemal spine on caudal vertebra 6).

Synapomorphic for *O. cubicus, O. cyanurus, O. whitleyi* is 28-2 (pterosphenoid projection absent).

Synapomorphic for *O. nasus* and *O. rhinorhynchus* are five character states: 13-2 (prootic shaft and ventral keel partly fused along distal margin); 32 (ethmoid blade expanded) 37 (rod-like process of hyomandibula with ventral curvature); 39 (ectopterygoid laterally rotated); 79-2 (dorsolateral processes of caudal vertebra 5 dorsally expanded and partly fused).

Synapomorphic for *Lactoria* species are eight character states: 16 (frontals form distinct arch over orbits); 19 (lateral ethmoid groove more lateral in position); 31 (ethmoid/lateral ethmoid junction concave); 80-2 (haemal spine lateral projections of caudal vertebra 5 overlap base of last and basal pterygiophore); 81 (haemal spine of caudal vertebra 5 reduced); 86-2 (haemal spine of caudal vertebra 6 is elongated with the distal end angled anteriorly); 88-1 (haemal spine of caudal vertebra 6 with well developed pair of ventrolateral processes); 104 (base of last anal basal pterygiophore dorsally expanded).

Synapomorphic for *L. cornuta, L. fornasini, L. reipublicae, L. gibbosus, L. concatenatus* is 88-2 (ventrolateral processes of caudal vertebra 6 joined posteriorly around base of last anal basal pterygiophore).

Synapomorphic for *L. fornasini, L. reipublicae, L. gibbosus, L. concatenatus* are three character states: 70-1 (neural spine of caudal vertebra 3 reduced); 72-1 (neural spine of caudal vertebra 4 reduced); 78-1 (neural spine of caudal vertebra 5 reduced).

Synapomorphic for *L. reipublicae, L. gibbosus, L. concatenatus* are seven character states: 70-2 (neural spine of caudal vertebra 3 absent); 72-2 (neural spine of caudal vertebra 4 absent); 78-2 (neural spine of caudal vertebra 5 absent); 85 (neural spine of caudal vertebra 6 reduced); 90-2 (autogenous dorsolateral processes of caudal vertebra 7 enlarged and angled anteriorly); 92-2 (autogenous dorsolateral processes of caudal vertebra 8 enlarged and angled anteriorly); 97 (anterolateral margin of centrum hypural plate anteriorly expanded).

Homoplastic Character States.—Of the 108 characters used in the analysis (but excluding #'s 52, 54, see below), 27 are hypothesized to display homoplastic states; of these 10 show no particular trend, four hypothesize an alternative resolution within *Lactoria,* and 13 are interpretable as parallelisms or reversals.

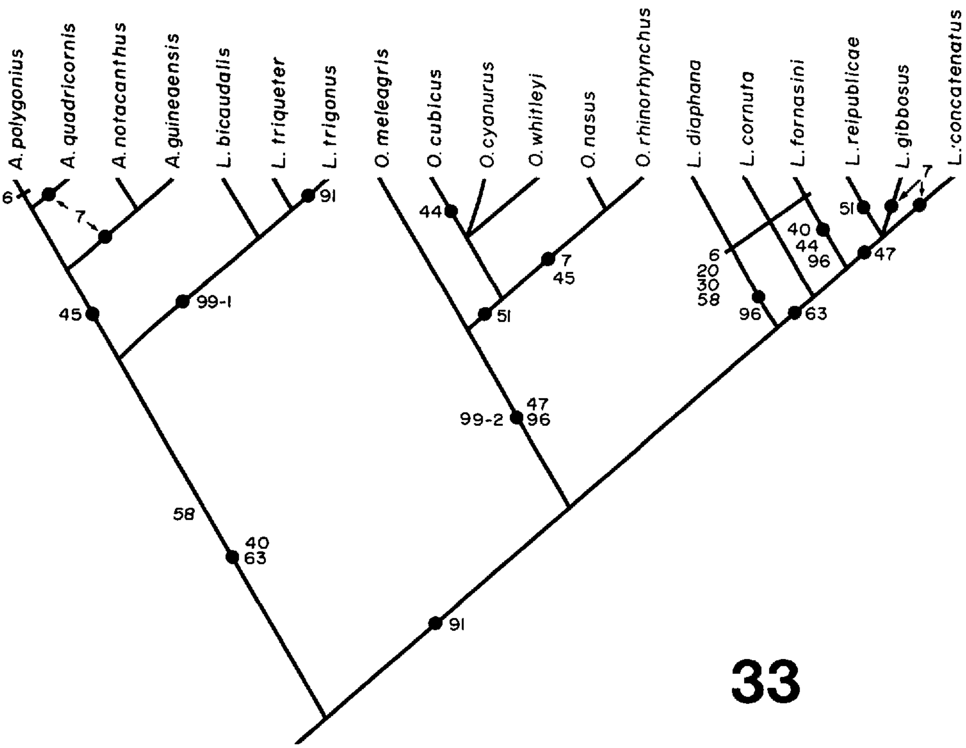

Figure 33. Phylogeny reconstruction for the 19 Ostraciinae species studied. Superimposed on the cladogram are homoplastic character states showing no particular trends and states showing alternate resolution within *Lactoria* (states 6, 20, 30, 58, identified by hash marks, for explanation see text and Fig. 32d).

Homoplastic character states showing no consistent trend are (Fig. 33): 7 (sphenotic ridge expanded laterally); 40 (mesopterygoid bulge absent); 44 (posterior point of subopercle elongate); 45 (posterior projection of preopercle recurved ventrally); 47 (joint ceratohyal/epihyal depression); 51 (tooth plate on second pharyngobranchial straight); 63 (ventrolateral processes of abdominal vertebrae 2 and 3 fused); 91 (reduced haemal spine of caudal vertebra 7); 96 (vertical ridge on anterolateral surface of centrum-hypural plate); 99 (extent of posterior expansion of last dorsal basal pterygiophore).

Homoplastic character states hypothesizing an alternative resolution within *Lactoria* are (Fig. 33): 6 (sphenotic ridge with ventral projection); 20 (lateral ethmoids with medially directed distal ridge); 30 (posterior of ethmoid shaft flared); 58 (process on posterior edge of coracoid absent).

Homoplastic character states interpretable as reductions are (Fig. 34, hypothesized as parallelism; Fig. 35, hypothesized as reversal): 29 (concave indentation between blade and shaft of ethmoid); 55 (shelf evident ventral to cleithrum pyramid); 60 (centra of abdominal vertebrae 2 and 3 fused); 61 (neural arches of abdominal vertebra 3 not joined); 71 (small, triangular dorsolateral process on caudal vertebra 3); 73 (enlarged dorsolateral process on caudal vertebra 4); 74 (short, broad pair of ventrolateral processes on caudal vertebra 4); 75 (neural spines of caudal vertebrae 3 and 4 joined); 76 (dorsolateral processes of caudal vertebrae 3 and 4 joined); 79 (well developed dorsolateral processes on caudal

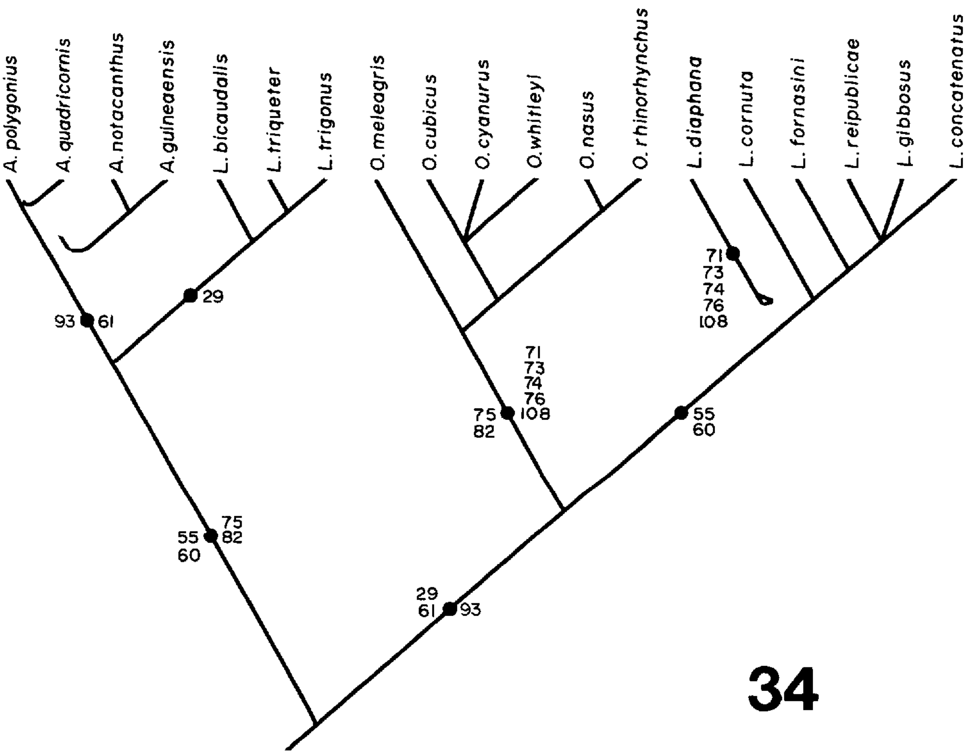

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Figure 34. Phylogeny reconstruction for the 19 Ostraciinae species studied. Superimposed on the cladogram are homoplastic character states interpretable as reduction. Character state distribution consistent with a hypothesis of parallel evolution.

vertebra 5); 82 (neural spines of caudal vertebrae 4 and 5 joined); 93 (haemal spine of caudal vertebra 8 not autogenous); 108 (ossified flange of last anal basal pterygiophore joined to ventral surface of caudal vertebra 4).

Unordered Character States.—Of the 18 multistate characters, two are treated a priori as unordered (see character state descriptions): 52 (Baudelot's ligament), and 54 (cleithrum pyramid). Optimizing Baudelot's ligament (three derived states) onto the existing cladogram results in four steps. Character state 52-1 (anterodorsal component fully ossified but not fused medially) is synapomorphic for all ostraciines; 52-3 (dorsolateral component completely unossified) is synapomorphic for *Ostracion* species. *Lactoria* appears to be polymorphic with *L. cornuta* and *L. gibbosus* sharing the homoplastic state 52-2 (dorsolateral component partially ossified). I was unable to determine the condition for *L. fornasini.* Optimizing the cleithrum pyramid (three derived states) resulted in three steps with 54-1 (pyramid narrow with median ridge) synapomorphic for *Lactoria* species, 54-2 (pyramid wide and rounded without median ridge) synapomorphic for all Atlantic ostraciines, and 54-3 (pyramid wide and rounded with median ridge) synapormorphic for *Lactophrys* species (Fig. 36).

The remaining 16 multistate characters were initially polarized according to the reasoning outlined in the character state descriptions. Treating these characters as unordered resulted in some minor differences in the interpretation of Ostraciinae relationships (Fig. 36).

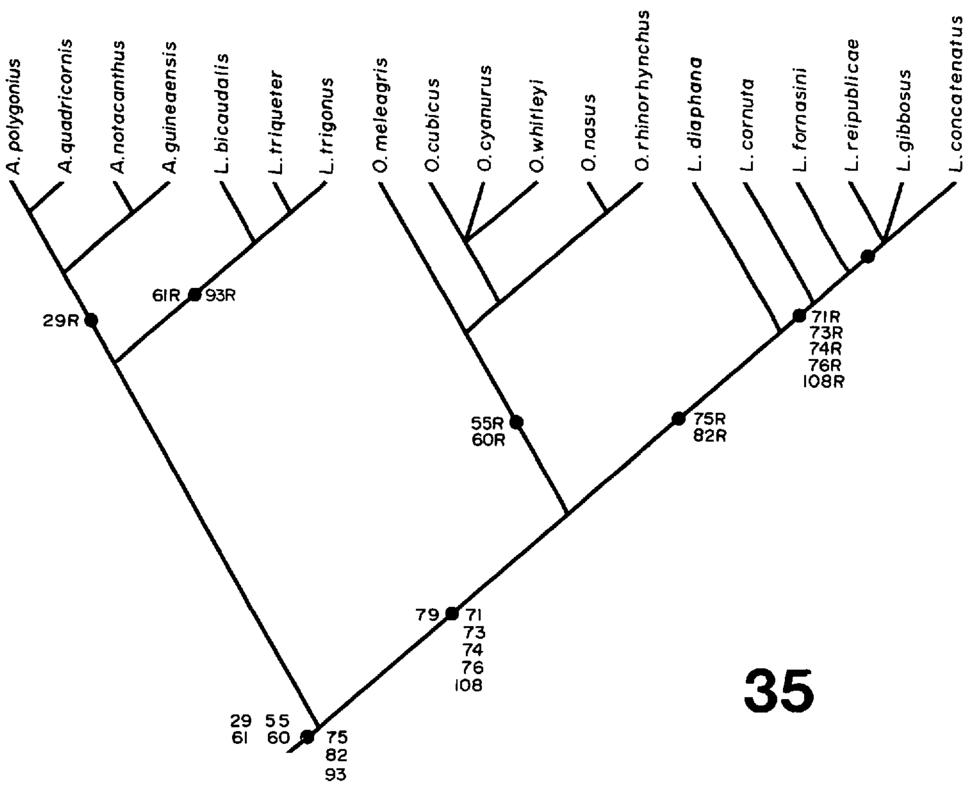

Figure 35. Phylogeny reconstruction for the 19 Ostraciinae species studied. Superimposed on the cladogram are homoplastic character states interpretable as reduction. Character state distribution consistent with a hypothesis of reversal.

Eight characters displayed the same polarity decisions as originally hypothesized: 13 (modifications to prootic suborbital shelf); 24 (joint between parasphenoid and vomer); 28 (modifications to parasphenoid interorbital keel); 79 (modification to dorsolateral processes of caudal vertebra 5); 80 (modification to haemal spine of caudal vertebra 5); 90 (modification to dorsolateral processes of caudal vertebra 7); 92 (modification to dorsolateral processes of caudal vertebra 8); 99 (modification to posteroventral edge of last dorsal basal pterygiophore).

Four characters were not unequivocally resolvable, but did not affect topology: 17 (anterior extent of frontals); 41 (modification to operculum); 53 (modification to dorsal half of cleithrum); 86 (modification to dorsolateral processes of caudal vertebra 6).

Four characters were optimized differently: 70 (modification to neural spine of caudal vertebra 3); 72 (modification to neural spine of caudal vertebra 4); 78 (modification to neural spine of caudal vertebra 5); 88 (modification to ventrolateral processes of caudal vertebra 6). These are associated with the previously mentioned character states hypothesizing an alternate resolution within *Lactoria*. In the first three cases reduction (70-1, 72-1, 78-1) and loss (70-2, 72-2, 78-2) are hypothesized to have occurred independently in *L. fornasini* and the common ancestor of *L. reipublicae, L. gibbosus,* and *L. concatenatus,* respectively. In the last case loss (88-2) is hypothesized to have occurred before reduction (88-1) (Fig 36).

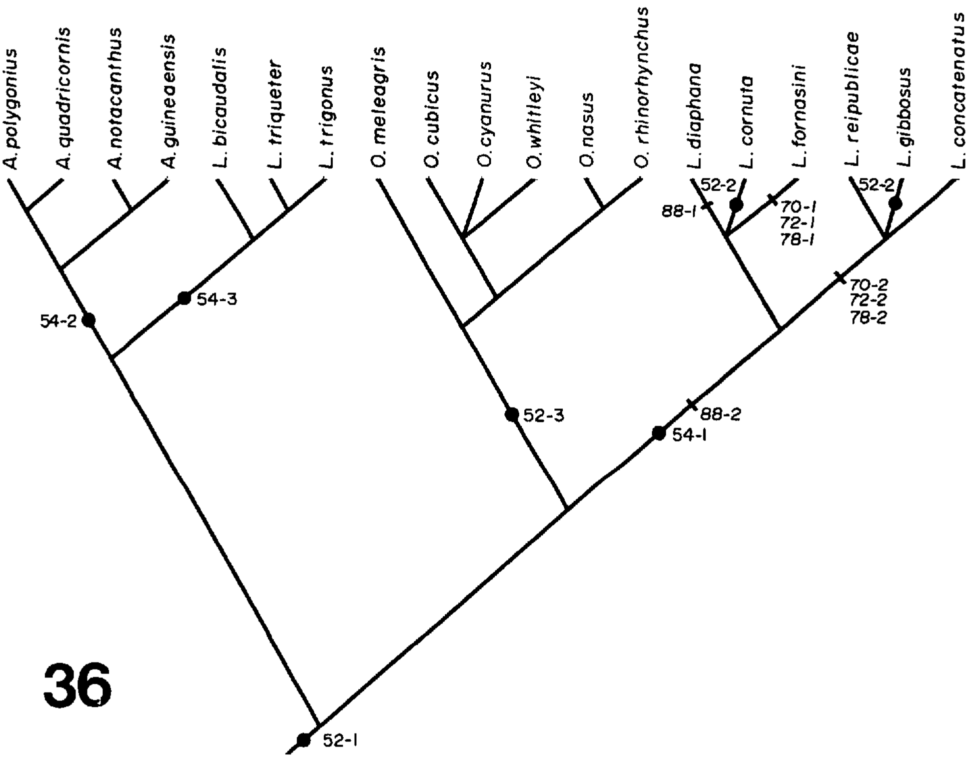

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Figure 36. Phylogeny reconstruction for the 19 Ostraciinae species studied. Superimposed on the cladogram are unordered character states. Dots represent states treated a priori as unordered, hash marks represent states resulting in alternate resolution after unordering.

(4) Biogeography

Distribution.—A summary of distribution patterns for the 19 species of Ostraciinae examined is presented below (Fig. 37). The summary is based on personal examination of material in five museum collections, augmented by records obtained from an additional 12 museums world-wide and literature records. Distribution maps for individual species, based on the above-mentioned museum collections, are not presented but are available from the author on request.

The four *Acanthostracion* species display a distinctly disjunct distribution (Tyler, 1965b). *A. polygonius* and *A. quadricornis* are distributed roughly sympatrically throughout the Caribbean (Caribbean plate) and adjacent North and South Atlantic coastlines (North American and South American plates, respectively); the distribution of *A. quadricornis* also extends to the Gulf of Mexico and Bermuda (North American plate); it was also found once in Algoa Bay, South Africa. *A. notacanthus* and *A. guineaensis* are found only in the eastern Atlantic (African plate). The range of *A. notacanthus* is apparently restricted to isolated populations off the Azores, St. Helena, and the Gulf of Guinea; *A. guineaensis* is recorded only from the Gulf of Guinea.

Lactophrys bicaudalis, L. triqueter, and *L. trigonus* are distributed roughly sympatrically with the Caribbean *Acanthostracion* species, with only isolated records from the Gulf of Mexico; *L. bicaudalis* is additionally absent from Bermuda.

Distribution of the Indo-Pacific ostraciines is characterized by overall sympatry

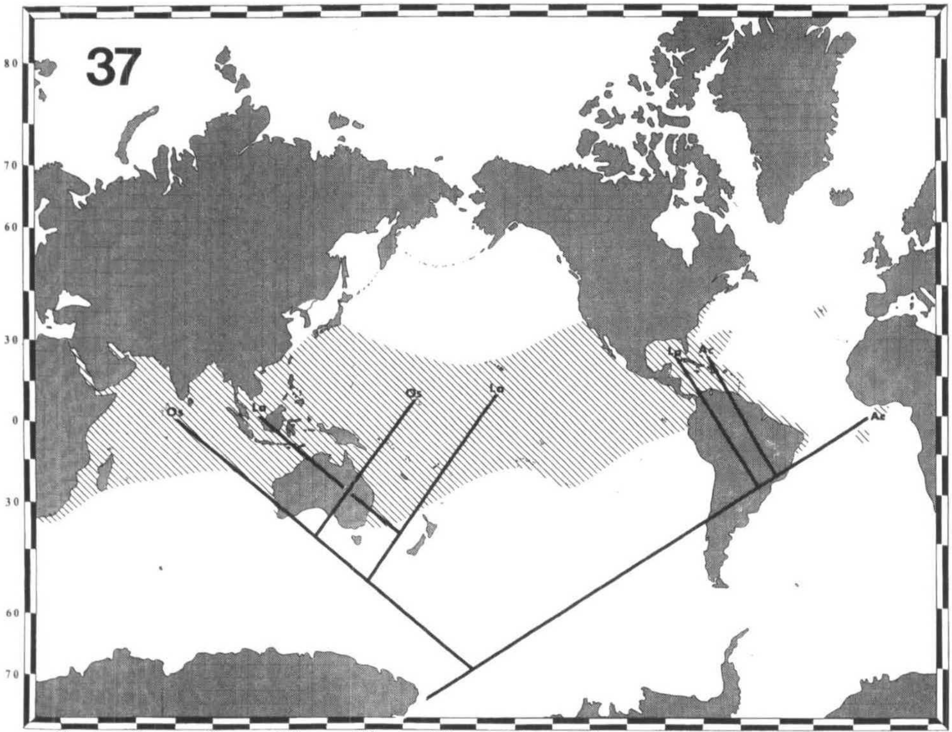

Figure 37. Combined distribution for all 19 Ostraciinae species studied. Superimposed are hypothesized area relationships. Placement of terminal nodes is arbitrarily based on estimates of centers of distribution based on concentration of records. Os = *Ostracion,* La = *Lactoria,* Ac = *Acanthostracion,* Lp = *Lactophrys.*

among species and disjunct populations within species. *Ostracion* and *Lactoria* show similarities in distribution in both widespread species and species of restricted distribution.

Widespread species of *Ostracion* are [*O. meleagris* (including "*O. camurum,*" "*O. lentiginosum,*" "*O. punctatus,*" "*O. oahuensis,*" "*O. orcus,*" and "*O. sebae*"), and *O cubicus* (including "*O. argus,*" "*O. immaculatus,*" and "*O. tuberculatus*")] and species with restricted distributions [*O. cyanurus, O. whitleyi* (including "*O. ornatus*" and "*O. solorensis*"), *O. nasus,* and *O. rhinorhynchus*]. *Ostracion meleagris* has a similarly broad distribution pattern to that of *L. diaphana* except that it is also found in the Indian Ocean proper (excluding the Arabian plate) and has not been recorded from the eastern Pacific north of the Baja Peninsula, California. The distribution of *O. cubicus* overlaps to a large extent with that of *O. meleagris*; *O. cubicus* has, however, not been reported from the eastern Pacific but has been recorded from the Red Sea and Persian Gulf.

Ostracion cyanurus has a disjunct distribution, having only been reported from the Arabian plate and the Caroline Islands. The remaining *Ostracion* species occur sympatrically in the region bounded by Australia, the Philippine Islands, Sumatra, and New Guinea. *Ostracion whitleyi* and *O. nasus* also share disjunct distributions on the Pacific plate (the former off Hawaii and Society Islands and Tuamotu, the latter only from Tuamotu) and African plate (Mauritius). In addition, *O. nasus* and *O. rhinorhynchus* are also recorded from India; and *O. rhinorhynchus* from Japan.

Lactoria species display two different but overlapping distribution trends, widely distributed throughout the Indo-Pacific [*L. diaphana* (including "*L. schlemmeri*"), *L. cornuta,* and *L. fornasini* (including "*L. galeodon*" and "*L. pentacanthus*")] and restricted [*L. reipublicae, L. gibbosus* "*O. turritus*"), and *L. concatenatus* (including "*O. stellifer*")]. Among the widespread species, *L. diaphana* has the greatest apparent longitudinal range, extending from the southeast coast of Africa (African plate) through Australia (Indo-Australian plate) and Japan to the west coast of southern North America and Central American (Pacific, Cocos, and Mazca plates). It has, however, not been recorded from the northern Indian Ocean or from the triangle bounded by Sumatra, New Guinea, and the Philippine Islands. In contrast, *L. cornuta* and *L. fornasini* have been recorded from localities throughout the Indian Ocean (with the notable exception of the Red Sea and the Persian Gulf) and the 'triangle,' but are absent from the Pacific coast of the Americas.

Distribution of the remaining *Lactoria* species appears more restricted. All appear to share with *L. cornuta* and *L. fornasini* the range between Australia and Japan; with *L. reipublicae* recorded only from isolated localities. *L. gibbosus* and *L. concatenatus* are also recorded from from the northern Indian Ocean to the east coast of Africa. *Lactoria gibbosus* is the only *Lactoria* species recorded from the Red Sea and Persian Gulf (Arabian plate).

Area Relationships.—Area relationships of ostraciines are very complicated (Fig. 37). Uncovering these relationships is made difficult by the sympatric distributions of all but two pairs of sister taxa: within *Acanthostracion,* the western Atlantic species (*A. polygonius* and *A. quadricornis*) are separated from their eastern Atlantic sister group (*A. notacanthus* and *A. guineaensis*) by the widening Atlantic Ocean. Within the Ostraciinae, the Atlantic ostraciines (*Acanthostracion* and *Lactophrys*) are separated from their Indo-Pacific sister group (*Ostracion* + *Lactoria*) by the Panamanian Isthmus on the one hand, and the closure of the ancient Tethys on the other. Further area relationships are not unequivocally recoverable.

DISCUSSION

Character Evolution

In interpreting the phylogenetic analysis of Ostraciinae relationships, I will concentrate on three aspects: interpretation of hypothesized homoplastic character states, of polarity decisions for multistate characters, and recognition of potential character complexes. Discussion of these aspects will be conducted to a large extent in the context of often hypothesized reductive trends in tetraodontiform character evolution.

As noted earlier, reductive characters appear to be widespread (if not dominant) in the evolutionary history of higher taxa within the Tetraodontiformes (Gregory, 1933; Tyler, 1963, 1970, 1980; Rosen, 1984, etc.). Indeed, Myers (1958) considered it a major mechanism in the evolution of teleost fishes. Tyler (e.g., 1980) argued that this trend has continued within the Ostraciinae, in particular with regards to caudal and precaudal vertebral elements. The analyses presented here have revealed that reduction (whether considered real or merely assumed) has had a profound effect on the interpretation of relationships among Ostraciinae taxa. From character recognition, to character state polarity decisions, to reconstruction and interpretation of phylogenetic relationships, reduction appears to present a common theme. Therefore, the effects of reductive characters (real or assumed) on recognition (and interpretation) of homoplasy, on polarity decisions for multistate characters, and on the recognition of 'trends' in character complexes will be explored.

Homoplastic Characters.—Of the 10 hypothesized homoplastic character states showing no particular trends (that is, no particular grouping emerged in the sense of a clique analysis), five [40 (mesopterygoid bulge absent), 44 (posterior point of subopercle elongated), 51 (tooth plate on second pharyngobranchial straight), 91 (reduction of haemal spine of caudal vertebra 7), 96 (vertical ridge on anterolateral surface of centrum-hypural plate)] are consistent in that each is hypothesized as synapomorphic for a recognized clade in addition to showing up elsewhere in a single terminal taxon (two for 96) (Fig. 33). It is tempting to conclude that the observed state in each of the single terminal taxa was a mistake, due either to mistaken identification or misinterpretation of homology. Similarly, the distribution of characters 45 (posterior projection of preopercle recurved ventrally) and 47 (joint ceratohyal/epihyal depression), each of which is apparently synapomorphic for two independent clades, leads to the conclusion that homoplasy is attributable to mistaken assumption of homology. In not one of these cases, however, do the present data provide an unequivocal solution beyond the above-mentioned argumentation which is based solely on an assumption of parsimonious evolution.

Character 99 (extent of posterior expansion of last dorsal basal pterygiophore) is problematic for two reasons. The polarity decision of this multistate character would lead one to conclude that the first derived state was reversed in *Acanthostracion* species (a reductive character?). Conclusions about this character are further complicated by the inability to determine which state is present in *Lactoria* species. This is not due to insufficient data, but, the fact that bones associated with the last dorsal basal pterygiophore in other ostraciine species are reduced or absent in *Lactoria* species.

The homoplastic character 7 (sphenotic ridge expanded laterally) is unique in two ways; it results in four additional steps to the cladogram, and its distribution results in two alternate hypotheses of relationships among ostraciine taxa (Fig. 32b, c). First is the resolution of the trichotomy involving *L. reipublicae, L. gibbosus,* and *L. concatenatus* such that the latter two species are considered sisters to the exclusion of the former. Second is the alternate resolution of *Acanthostracion* species relationships with *A. quadricornis* hypothesized to be the sister group to *A. notacanthus* + *A. guineaensis.* I have rejected both of these alternative resolutions. My reasoning is simple: if homoplastic character states are recognized as problematic (which I assert is axiomatic until such time as they have been reexamined), then there can be no justification for accepting putative clades based on such characters alone; character states which are hypothesized as homoplastic can not, by definition, simultaneously be synapomorphies (which follows from Hennig's 'Grouping Rule').

Among the other characters with homoplastic states, four [6 (sphenotic ridge with ventral projection), 20 (lateral ethmoids with medially directed distal ridge), 30 (posterior of ethmoid flared), 58 (protrusion on posterior edge of coracoid absent)] are particularly interesting (Figs. 32d, 33). They support an alternative hypothesis of relationships among *Lactoria* species with *L. diaphana, L. cornuta,* and *L. fornasini* together forming the sister group to *L. reipublicae, L. gibbosus,* and *L. concatenatus* (one implication of this alternate hypothesis of relationships will be discussed in the section on multistate characters). However, all but one of these characters (state 30) is problematic in some other way. Character state 6 also occurs in *A. polygonius* and state 58 in all *Acanthostracion* species, and presence of state 20 is unknown for *L. fornasini.* Thus, support for this alternate hypothesis is considerably weakened.

The majority of the remaining hypothesized homoplasies (12 of 13) have been assigned one of two equally parsimonious arrangements on the cladogram: multiple (i.e., duplicate) independent origin (Fig. 34) or single origin with subsequent reversal (Fig. 35). Parsimony-based algorithms are incapable of distinguishing between these alternatives. Distinction is, however, possible if we assume that a mistake in coding has been made (in this context, polarity decisions are not in question; recognition of apomorphic character states is based on the outgroup method of Watrous and Wheeler [1981, see also Maddison et al., 1984], and thus are considered as robust as possible in the context of modern cladistic methodology). Accordingly, independent origin is reinterpreted as separated characters (apomorphic character state incorrectly coded as homologous), and reversal is reinterpreted as a reduction transformation series (plesiomorphic character state incorrectly coded as homologous). There are biological sources of evidence to help distinguish between these alternative reinterpretations: ontogeny and correlation with other, non-homoplastic characters.

Ontogenetic data are circumstantial only, but favor the reduction hypothesis: among *Lactoria* species, some juvenile specimens of *L. cornuta* and *L. fornasini* possess dorsolateral processes which, in proportion to vertebral size, are larger than those in the adults. Many more juvenile specimens (optimally, a series of incremental size increase) than were available will have to be examined. Correlation with other characters also tends to favor reduction. In particular, the correlated reduction/loss of neural spines of caudal vertebrae 3 to 5 and subsequent increase in dorsolateral processes of caudal vertebrae 6 to 8 among *Lactoria* species indicates a series of larger-scale modifications to the posterior precaudal skeleton that is consistent with reduction for these hypothesized homoplastic caudal elements.

Multistate Characters.—Two of the 18 multistate characters could not be polarized even though states were clearly recognized. Polarizing the states of Baudelot's ligament (character 52) proved particularly difficult. In all non-ostraciid tetraodontiforms the ligament is considered non-ossified and neither Tyler (1968, 1980) nor Matsuura (1979) made any mention of it outside the Ostraciidae. Winterbottom and Tyler (1983) considered ossification of the ligament synapomorphic for ostraciids. I have found, however, that the ligament actually consists of two components, both of which are ossified in the Aracaninae but only one (or neither) in the Ostraciinae, and then not always completely. Because of this observed difference in degree of ossification between ostraciines and aracanines (and the absence in other tetraodontiforms) the outgroup polarization method cannot be applied to its character states. When treated as unordered, a single ossified limb is hypothesized to be synapomorphic for the ingroup, with subsequent reduction in *Ostracion* species. Partial reduction observed in two *Lactoria* species complicates the picture but also indicates that the reduction trend may involve all Indo-Pacific ostraciines. Irrespective of whether a single ossified limb or complete ossification will eventually be determined to be synapormorphic for all ostraciids, character state distribution among ostraciines is consistent with a hypothesis of reduction (Fig. 36).

Modification of the cleithrum pyramid (character 54) was by the same token not considered reductive. Optimization of the three apomorphic states results in the conclusion that two characters are involved, evolving independently in Atlantic ostraciines (development of a large, broad, and rounded pyramid) and *Lactoria* species (development of a small, narrow, and pointed pyramid). Presence of the pyramid could not be hypothesized to be synapomorphic for all ostraciines without invoking subsequent reduction in *Ostracion* species, and therefore additional homoplasy. Note, however, that another character (55—shelf evident ventral to cleithrum pyramid) is considered homoplastic because of its presence in Atlantic ostraciines and *Lactoria* species (the same distribution is observed for character 60—centra of abdominal vertebrae 2 and 3 fused, see discussion of character complexes). It is one of the group of characters whose hypothesized homoplasy may be attributed to misidentification of apomorphic loss with plesiomorphic absence. If the latter is correct then the interpretation of evolution of pyramid shape may be more complex than presently proposed (Fig. 36).

Treating the remaining 16 multistate characters as unordered resulted in only four characters with conflicting interpretations of transformations from those originally proposed (Fig. 36). These four characters [70 (modification to neural spine of caudal vertebra 3), 72 (modification to neural spine of caudal vertebra 4), 78 (modification to neural spine of caudal vertebra 5), 88 (modification to ventrolateral processes of caudal vertebra 6)] have all been reinterpreted specifically due to the hypothesis that *Lactoria diaphana, L. cornuta,* and *L. fornasini* are monophyletic to the exclusion of the other *Lactoria* species based on characters 6, 20, 30, and 58 (Fig. 32d). Since these multistate characters are the primary support for the proposed relationship among *Lactoria* species (Fig. 32a), it is hardly surprising that treating them as unordered results in their reinterpretation based on that group of characters that originally conflicted with them (see above discussion on homoplastic characters). The fact that three of the four characters supporting the alternate hypothesis (on which the unordered multistate characters are reinterpreted) have homoplastic states unrelated to the question of *Lactoria* species relationships leads me to conclude that optimizing the multistate characters on the resolution provided by these characters (or any resolution based on homoplastic characters) is unjustified.

Of these 16 multistate characters only 6 are explicitly reductive. This indicates that reduction per se is not a dominant trend in interpreting character evolution among ostraciine multistate characters; a conclusion which is, incidentally, not affected by the alternate optimization of the four characters just mentioned.

Character Complexes.—Character complexes are of particular interest because they can often be mistaken for single, multistate characters whose states are causally linked. This is probably the case because character complexes can only be recognized as being such a posteriori. When a recognizable "endproduct" is reached we cry eureka! and start to reconstruct the necessary steps which lead to such a magnificently complex feature. Belief in anagenetic change and progressive evolution has resulted from such "hindsight" approaches to evolution. Dawkins (1986) very eloquently described the fallacy of this outlook using the classic example of the vertebrate eye. At least one complex interpreted in a similarly progressive manner, the fusion complex of anterior abdominal vertebrae, has been recorded for ostraciines. I have dissected the components of this and two other complexes to determine how closely such reconstructions resemble the above mentioned a priori expectations and what role reduction plays in such interpretations.

Tyler (1963) pointed out that earlier workers consistently underestimated the number of vertebral elements in ostraciids. He demonstrated that these workers counted as the first abdominal vertebra a complex of from two to five vertebrae; a complex reduced by fusion. Tyler (1963) described the fusion characteristics of the first five vertebrae in *Acanthostracion quadricornis*. He observed for the smallest (8.2 mm) juvenile specimens that the first two centra fused with one another and with basioccipital, and the third and fourth fused their centra but not with anterior (1+2) or posterior (5) centra. With increasing size (15.3 mm and 25 mm) the centra, neural arches and ventrolateral processes continued to join until, in adults, the elements were indistinguishable, giving the mistaken impression of a single vertebra. Tyler compared these results with material from other ostraciid species, concluding that in aracanines only the first two centra were fused, in *Lactoria* and *Ostracion* species vertebrae 3 and 4 were also fused to the anterior elements, and that in *Acanthostracion* and *Lactophrys* all five vertebral centra were fused. Tyler (1980) used the distinction between 4 and 5 vertebrae in the fusion complex as a distinguishing character between *Lactoria* and *Ostracion* on the one hand and *Acanthostracion* and *Lactophrys* on the other. Winterbottom and Tyler (1983) used characters associated with the fusion complex as synapomorphic for the Ostraciidae (fusion of at least the first two vertebrae) and the Ostraciinae (first four or five vertebrae variously fused).

Tyler (1980) interpreted fusion in the anterior abdominal vertebrae as a linear transformation from 2 (Aracaninae) to 4 (Indo-Pacific Ostraciinae) to 5 (Atlantic Ostraciinae). Both the present study and Tyler's own work, however, shed doubt on this interpretation. I agree with Tyler's observation that all adult Atlantic ostraciines have the centra of the first five vertebrae fused, and that adults of *Lactoria* species have the first four fused. In addition to Tyler's (1980) observation on *Ostracion meleagris* and *O. cubicus* (reported by him as *O. lentiginosum* and *O. tuberculatus*, respectively), I have observed that the remaining *Ostracion* species also lack complete fusion between abdominal vertebrae 2 and 3. This character distribution makes it impossible for the vertebral fusion to have proceeded as a linear transformation unless *Ostracion* species subsequently reduced the fusion between the centra of vertebrae 2 and 3. The story is further complicated by Tyler's (1963) original observation that *Acanthostracion quadricornis* juveniles also lack fusion between centra 2 and 3; an observation I have been able to confirm for each species for which I had observed juvenile material (Appendix 2). Including the ontogenetic data would lead to the conclusion that a fusion complex of vertebrae 1+2 and 3+4 is plesiomorphic for osstraciines, not 1+2+3+4; that, further, the complete fusion of the first four vertebrae in *Lactoria* species and the first five in *Acanthostracion* and *Lactophrys* species are two independent events.

Another character complex also recognized by Tyler (1963, 1980) relates to modifications to vertebral elements of caudal vertebrae 3 to 8. Presence of neural spines is plesiomorphic within the Ostraciinae and their reduction/loss involves a series of apparently correlated apomorphic changes at different stages in the phylogeny. Correlated with these modifications (in the sense that these character states occur along the same branches of the phylogeny and can be considered in some way spatially and functionally related) is the reduction of the dorsolateral processes of caudal vertebrae 3 to 5 (this interpretation is based on their origin being synapomorphic for all Indo-Pacific ostraciines, see previous discussion on homoplastic characters), modification/enlargement of dorsolateral processes of caudal vertebrae 6 to 8, and reduction of the posteroventral extent of the last dorsal basal pterygiophore. Taken together, these modifications result in a radically altered overall morphology in the derived *Lactoria* species (*L. reipublicae, L. gibbosus*, and *L. concatenatus*). Functionally this appears to be associated with modification to the support structure of the dorsal fin; changes in the shape, distribution and function of associated muscles might also be expected (but see Winterbottom, 1974: 44–45).

The modifications just mentioned are similar to those associated with the anterior abdominal vertebrae in that reduction appears to play an important role. They differ in that reduction in the different characters appears to be linearly correlated as opposed to diverging. Additionally, reduction here has led to loss of characters whereas in the anterior abdominal vertebrae, reduction is associated primarily with fusion.

A third group of characters apparently associated in a complex gives rise to the diagnostic (Tyler, 1980) dorsoventrally compressed skull in Indo-Pacific ostraciines, in particular *Ostracion* species. Associated with this complex are the modification/reduction of the interorbital keel of the parasphenoid, reduction of the parasphenoid-pterosphenoid rod connection, anteroventral sloping of the posterior orbital wall formed by the pterosphenoid and prootic, modification of the prootic shelf, and dorsal and lateral expansion of sphenotic and pterotic. The ultimate result of these modifications is a reduction of the depth of the skull, decrease of the orbital volume contained within the skull, and lateral movement of the eyes.

Although this complex contains some characters with reductive states, most of the modifications involve alteration of shape of the associated bones without reduction or loss. In addition, the positions of the above mentioned modifications on the cladogram indicate that divergence rather than linear change resulted from the apomorphic changes in these characters.

These three examples demonstrate that evolution of character complexes, or more specifically the "resulting" feature, may involve either or both anagenetic and cladogenetic change. At least in the Ostraciinae, reduction can (but need not) be important in the development of such complexes, and reduction is not necessarily a purely linear phenomenon (i.e., indicative of progressive evolution).

Phylogeny Reconstruction

Higher Level Relationships.—In choosing the outgroups for the analysis of Ostraciinae relationships I followed the tetraodontiform family and subfamily relationships as proposed by Winterbottom (1974) and Winterbottom and Tyler (1983) (Fig. 1). Given this relationships among the outgroup taxa, characters states coded as derived for the Tetraodontidae (chars. 71, 73, 79, 86, 90, 92) are interpreted as parallelisms. There are, however, alternate views about the position of ostraciids which may affect this interpretation (i.e., Leis, 1984; Rosen, 1984).

Initially, when comparing alternate hypotheses of higher-level relationships, I considered only the topologies, thinking them valid alternatives. But examination of supporting evidence showed the flaw in this approach: whereas Winterbottom (1974) and Winterbottom and Tyler (1983) based monophyly of the Balistoidea (including Ostraciidae) on 20 osteological and myological characters (and monophyly of Tetraodontoidea on 15 myological characters), Leis (1984) placed the Ostraciidae in the Tetraodontoidea based on a total of 14 early life history characters (two uniting Balistoidea), and Rosen's (1984) cladogram placed the Ostraciidae in the Tetraodontoidea on the basis of a single osteological character. Parsimony analysis based on a combination of the above characters unequivocally favors the hypothesis of Winterbottom (1974) and Winterbottom and Tyler (1983).

I have already examined some of the characters used by Winterbottom and Tyler (1983, see results section). Of Leis's 14 characters, he acknowledges that four (2, 6, 11a, and 21a) involve questionable polarity decisions, and four (10b, 11b, 15, 21b) display homoplasy in the analysis. In addition (and I recognize the difficulty of obtaining material), Leis had only a very limited number of ostraciine species to work with (and no aracanines). It is, therefore, hardly justified to consider Leis's (1984) topology as evidence equivalent to that of Winterbottom (1974) and Winterbottom and Tyler (1983). Rosen's only character, aside from being outweighed 35 to 1, was based on several (questionable, but not necessarily inaccurate) assumptions of homology. I would contend, furthermore, that his 'character' is actually a complex of characters, each of which must be shown to have homologous states in ostraciines and tetraodontoids before his 'character' can even be considered valid, let alone outweighing the contradictory osteological and myological evidence. For instance: is the reduction of spines homologous: What role does the first pterygiophore of ostraciines play (Tyler's supraneural)—is it a fusion product? What about the number of pterygiophores and rays in the various taxa? Is the position of the first pterygiophore relative to vertebral counts phylogenetically informative? Is this pterygiophore even homologous among taxa?

Weighing the evidence, there can be no question that Ostraciinae and Aracaninae are sister taxa (a proposal that has never been disputed) and that in spite of the assertions of Leis (1984) and Rosen (1984) the Ostraciidae and Balistidae are also sister taxa.

Relationships within Ostraciinae.—Only two (tentative) phylogeneies have been proposed for taxa within the Ostraciinae, and only at the generic level (Tyler, 1980; Mok, 1974). Mok's (1974, unpubl.) phylogeny was based on certain aspects of gut morphology, with the greatest amount of resolution based on differences in "gross intestinal convolution patterns." His vague analytical protocol, especially confusing reference to character state polarity decisions, makes it difficult to evaluate his conclusions. Tyler (1980) proposed a phylogeny very similar to the one proposed here. The important differences can be attributed to Tyler's use of both primitive and derived characters to recognize lineages (Tyler has never assumed his phylogenies to be cladistic). Tyler considered *Ostracion* and *Rhynchostracion,* and *Lactoria* and *Tetrosomus,* respectively, to be sister groups. In each of these relationships my analysis has led to the conclusion that the latter genus must be considered junior synonym of the former because recognizing the latter (*Rhynchostracion, Tetrosomus*) would render the former (*Ostracion, Lactoria*) paraphyletic. The same pattern is evident for *Lactophrys* species, although the decision to synonymize *Rhinesomus* with *Lactoria* has already been made (see Appendix 1).

Species level phylogenetic relationships in the Ostraciinae are, with minor exceptions, well resolved. There are three patterns, in particular, which deserve additional examination. Within *Acanthostracion* species, the sister group relationship between *A. polygonius* and *A. quadricornis* is based on a single character. This, and the observation that one of the homoplastic characters (character 7) offers an alternate interpretation, indicates that the proposed relationship requires further investigation. That same homoplastic character also purports to resolve the proposed trichotomy between *Lactoria reipublicae, L. gibbosus,* and *L. concatenatus.* Additional characters will have to be sought before accepting this problematic resolution. Another trichotomy exists between *Ostracion cubicus, O. cyanurus,* and *O. whitleyi.* This trichotomy is of interest because *Ostracion* species (excluding *O. nasus* and *O. rhinorhynchus*) are usually distinguished on the basis of color pattern differences which, with one exception (see below), are not supported by the osteological evidence. This is further emphasized by the observation that specimens associated with two of the junior synonyms most often recognized as valid (on the basis of color pattern) in the literature (*'O. lentiginosum,'* syn. of *O. meleagris*; *'O. immaculatus,'* syn. of *O. cubicus*) are osteologically indistinguishable from specimens associated with the senior synonym. Furthermore, all specimens examined at the Tokyo University Museum, labelled *O. immaculatus* (as the specific name indicates, it is distinguished from *O. cubicus* in lacking the conspicuous blue or black spots on yellow background), were found to possess faded but clearly visible spots over the entire carapace. If these were absent in freshly caught material but present in preserved material, it seems reasonable that these spots were masked (implying their presence) in at least adult populations around Japan. I submit that many of the color pattern differences (although interesting) may be no more than population level color morphs subject to environmental (e.g., nutritional) variation. Much taxonomic work needs to be conducted on *Ostracion* species, including geographic and ontogenetic variation, before this problem can be resolved.

Historical Biogeography

The overall sympatric distribution pattern of ostraciine species makes it very difficult to interpret their biogeographic history. Only two allopatric patterns were discerned, and interpretation of their history is not unequivocal. The distribution of *Acanthostracion* species on either side of the Atlantic (with *A. notacanthus* and *A. guineaensis* in the eastern Atlantic, and *A. polygonius* and *A. quadricornis* in the western Atlantic) is likely correlated with the widening of the Atlantic Ocean. The geographic origins of this relationship are likely in the Caribbean in the sister group relationship with *Lactophrys* species; these relationships are confused, however, because the western Atlantic *Acanthostracion* and *Lactoria* species are distributed sympatrically. Given the complexity of this region and previous attempts to resolve relationships of Caribbean taxa (Kluge, 1988; Rauchenberg, 1988; Liebherr, 1988) it seems unlikely that historical relationships among Atlantic ostraciine will be fully understood on the basis of phylogeny and current distribution pattern alone.

Similarly, the sister group relationship between Atlantic and Indo-Pacific ostraciines is reflected in their allopatric distribution. The historical reason for this distribution is even less clear. Since both lineages are monophyletic, the phylogeny is equivocal with respect to direction of relationship (as is the case within *Acanthostracion*). The Aracaninae are of little help, for although they are not found in the Atlantic (hinting at an Indo-Pacific origin), they are reportedly antitropically distributed, which is generally considered a derived condition. Furthermore, there are two conflicting vicariant scenarios to explain such a distribution in the absence of other evidence. (1) Tethyan origin with isolation of Atlantic and Mediterranean populations, and Indo-Pacific populations. Isolation occurring with closure of the Tethys. (2) Pacific plate origin with isolation of Indo-West Pacific and Atlantic populations. Isolation occurring with the first formation of the Panamanian Isthmus (as early as 100–80 mya, Smith et al., 1981). Present day distributions tend to favor the latter scenario as there are no natural populations of any ostraciine species recorded from the Mediterranean (Spanier and Goren, 1988). On the surface, fossil evidence tends to favor the former scenario because all fossil tetraodontiforms considered related to ostraciids (Tyler, 1973, 1980) have been recorded from the famous fish beds of Monte Bolca, Italy. These fossils have been deposited in the lower Eocene (~55–50 mya), leading Tyler (1980) among others to conclude that their presence supports a Tethyan origin of the Atlantic ostraciines via the Mediterranean). Unfortunately the fossils of *E. sorbinii* are preserved in such a way that the critical osteological characters are not visible. Thus the evidence provided by *E. sorbinii* is circumstantial at best and could with equal confidence (which is poor) be interpreted as a derived taxon within one of the ostraciine lineages. At present, interpretation of causal mechanisms underlying the historical biogeography of Indo-Pacific and Atlantic ostraciines must remain equivocal.

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APPENDIX 1

Selected references for Ostraciinae genera and species (not including changes made in present paper).

(1) *Acanthostracion* Bleeker, 1865

A. quadricornis (Linnaeus, 1758), type species
junior synonyms, sensu Tyler (1965): *Ostracion tricornis* Linnaeus, 1758; *O. lister* Lacépède, 1798; *O. maculatus* Hollard, 1857; *O. gronovii* Bleeker, 1865; *O. sexcornutus* Mitchill, 1880

A. polygonius Poey, 1876
jun. syn., sensu Tyler (1965): *Lactophrys saxatilis* Mowbray, 1931

A. notacanthus (Bleeker, 1863)

A. guineaensis (Bleeker, 1863)

(2) *Lactophrys* Swainson, 1839
jun. syns. sensu Golvan (1963): *Rhinesomus* Swainson, 1839; *Chapinus* Jordan and Everman, 1896; *Triorus* Jordan and Hubbs, 1925

L. trigonus (Linnaeus, 1758), type species
jun. syns., sensu Günther (1873): *L. yalei* Dekay, 1861; *L. oviceps* Kaup, 1855

L. triqueter (Linnaeus, 1758)

L. bicaudalis (Linnaeus, 1758)

(3) *Ostracion* Linnaeus, 1758
jun. syns., sensu Golvan (1963): *Cibotion* Kaup, 1855; *Goniodermis* Rafinesque, 1815

O. cubicus Linnaeus, 1758, type species
jun. syns., sensu Günther (1873): *O. immaculatus* Temnick and Schlegel, 1850; *O. tuberculatus* Linnaeus, 1758; *O. argus* Rüppell, 1828; *O. tetrogonus* Linnaeus, 1758; *O. tesserula* Cantor, 1849; *O. auricauda* Seale, 1906. Additionally, sensu Fowler (1928, reprinted 1967): *O. pulul* Thiollière, ... ; *O. chryseres* Seale, 1906

O. meleagris Shaw, 1796
jun. syns. sensu Günther (1873, reprinted 1966), Fowler (1928, reprinted 1967; see also Barnard, 1927; Smith, 1961): *O. punctatus* Bloch and Schneider, 1801; *O. lentiginosus* Bloch and Schneider, 1801; *O. sebae* Bleeker, 1851; *O. pointillé* Lacépède, 1798; *O. bombifrons* Hollard, 1857; *O. camurum* Jenkins, 1903; *O. oahuensis* Jordan and Everman, 1898

O. cyanurus Rüppell, 1828

O. whitleyi Fowler, 1931
jun. syns., sensu Tinker (1978; see also Munro, 1967): *O. ornatus* Hollard, 1857; *O. solorensis* Bleeker, 1853; *O. renardi* Bleeker, 1856

O. trachys Randall, 1975

(4) *Rhynchostracion* Fraser-Brunner, 1935

R. nasus Bloch and Schneider, 1801, type species

R. rhinorhynchus Bleeker, 1852

(5) *Lactoria* Jordan and Fowler, 1902

L. cornuta (Linnaeus, 1975), type species
jun. syns. sensu Günther (1873, reprinted 1966; see also Fowler, 1928, and Smith, 1961): *O. arcus* Bleeker, 1863; *O. corentis* Linnaeus, 1758; *O. valentini* Bleeker, 1863

L. diaphana (Bloch and Schneider, 1846)
jun. syns., sensu Günther (1873, reprinted 1966; see also Fowler, 1928, and Smith, 1961): *O. brevicornis* Schlegel, 1858; *O. undecim-aculeatus* Smith, 1847; *O. schlemmeri* Jordan and Evermann, 1898; *O. dexteri* Seale, 1906; *O. paschae* Rendahl, 1927

L. fornasini (Bianconi, 1846)
jun. syns., sensu Günther (1873, reprinted 1966; see also Fowler, 1928, and Smith, 1961): *L. fuscomaculatus* von Bonde, 1923; *L. galeodon* Jenkins, 1903; *O. pentacanthus* Bleeker, 1863

(6) *Tetrosomus* Swainson, 1839

T. gibbosus (Linnaeus, 1758), type species
jun. syn., sensu Smith (1961): *O. turritus* Forsskål, 1775

T. concatenatus (Bloch, 1786)
jun. syns., sensu Smith (1961): *O. bicuspis* Blumenbach; *O. stellifer* Bloch and Schneider, 1801

T. reipublicae (Ogilby, 1913)

APPENDIX 2

Cleared and stained material examined for osteological characters (number in brackets following catalogue numbers represents number of specimens in lot, "juv." indicates that juvenile specimens were examined).

(1) Outgroup taxa: Tetraodontidae, material examined: *Torquigener leucogramma* ROM 765CS (3); Diodontidae, material examined: *Diodon* species ROM 368CS (1), *Diodon holacanthus* ROM 1438CS (1); Balistidae, material examined: Unknown species ROM 564CS (1), *Balistes vetula* ROM 527CS (1), *Rhinecanthus aculeatus* ROM 672CS (2), ROM 1123CS (1), *Monacanthus ciliatus* ROM 789CS (4); Aracaninae, material examined: *Aracana aurita* ANSP 109572 (1), *Aracana ornata* ANSP 33173 (1), ANSP 109570 (1)

(2) Ingroup taxa: *Acanthostracion polygonius* Material examined: ANSP 83840 (1), ANSP 80008 (1), CAS(SU) 51172 (1, juv.), CAS(SU) 51173 (1); *Acanthostracion quadricornis* Material examined: ANSP 102749 (1), ANSP 103506 (1), ANSP 109631 (1), ANSP 98614 (1), ANSP 98616 (1), ANSP 98615 (1), ANSP 98617 (2), ANSP 98618 (1), ANSP 98843 (2), CAS 31990 (2, juv.); *Acanthostracion notacanthus* Material examined: ANSP 102909 (1), ANSP 102910 (1); *Acanthostracion guineaensis* Material examined: ANSP 102874 (1), ANSP 106786 (1); *Lactophrys bicaudalis* Material examined: ANSP 70147 (1), ANSP 85199 (1, as "*Rhinesomus*" *bicaudalis*); *Lactophrys triqueter* Material examined: ANSP 91385 (1), ANSP 98625 (2, as *Rhinesomus triqueter*), USNM 301962 (1, juv.); *Lactophrys trigonus* Material examined: ANSP 49179 (2, as *L. tigrinus*), ANSP 74890 (3), USNM 301963 (1, juv.); *Lactoria diaphana* Material examined: CAS(SU) 23437 (1, juv.), CAS 56611 (1), USNM 103761 (1, as *O. galeodon*); *Lactoria fornasini* Material examined: ANSP 104866 (2), ANSP 104837 (1), ANSP 89016 (2), ANSP 83863 (1), CAS(SU) 31755 (2, juv.); *Lactoria cornuta* Material examined: ANSP 98623 (1), ANSP 98621 (1), ANSP 98622 (1), ANSP 119262 (1, as *L. cornutas*), ANSP 98620 (1), ANSP 91662 (1, as *Ostracion cornutus*), CAS 9618 (1, juv.); *Ostracion meleagris* Material examined: ANSP 112738 (1, as *O. lentiginosum*), ANSP 98624 (1, as *O. lentiginosum*), ANSP 104875 (2, as *O. lentiginosum*), CAS 65167 (1, juv.); *Ostracion cubicus* Material examined: CAS 65168 (1), ROM 1392CS (2, juv.), USNM 71552 (1, as *O. immaculatus*), ANSP 104830 (1, as *O. tuberculatus*), ANSP 112942 (1, as *O. tuberculatus*), ANSP 112881 (1, as *O. tuberculatus*), ANSP 112904 (2, as *O. tuberculatus*); *Ostracion cyanurus* Material examined: ROM 1125CS (1), ROM 1391CS (1, juv.), ROM 1393CS (1); *Ostracion whitleyi* Material examined: ANSP 109815 (1); *Rhynchostracion nasus* Material examined: CAS 17699 (2, juv.); *Rhynchostracion rhinorhynchus* Material examined: CAS(SU) 29958 (1, juv.), ANSP 90158 (1, as *Ostracion rhinorhynchus*), ANSP 95825 (1, as *Ostracion rhinorhynchus*), ANSP 10137 (1, as *Ostracion rhinorhynchus*); *Tetrosomus reipublicae* Material examined: CAS 65166 (1), CAS 28772 (2, juv.); *Tetrosomus gibbosus* Material examined: ANSP 100818 (1), CAS 9727 (1, juv., as *Rhinesomus gibbosus*); *Tetrosomus concatenatus* Material examined: ANSP 104755 (1), USNM 6912 (1, juv.).