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**Phylogeny of Ammodytidae (Teleostei) with a study of their
scales**

**Radding, Joel Martin, Ph.D.
City University of New York, 1994**

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PHYLOGENY OF AMMODYTIDAE (TELEOSTEI) WITH A STUDY OF THEIR
SCALES

by

JOEL M. RADDING

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy, The City University of New York

1994

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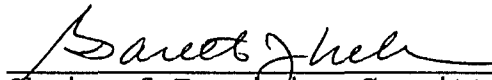
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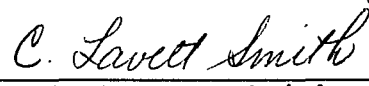
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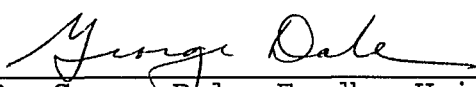
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Abstract

PHYLOGENY OF AMMODYTIDAE WITH A STUDY OF THEIR SCALES

by

Joel M. Radding

Adviser: Professor Gareth Nelson

Newly discovered characters shared by Trichonotidae and Ammodytidae, including highly elongate anterodorsal process on suboperculum, flattened supraoccipital with reduced crest and posterior scale field radial ridges ending as blunt spines on margin, provide evidence of their affinity. Uranoscopids and trachinids were previously proposed as the sister to Ammodytidae but these shared specializations move Trichonotidae into a polytomous relationship with Uranoscopidae plus Trachinidae, as the outgroup to Ammodytidae. The most plesiomorphic ammodytids are *Embolichthys mitsukurii* and *Bleekeria viridianguilla*, characterized by primitive lepidologies and dorsal fin anatomy but their monophyly is supported by synapomorphies describing number and morphology of extra labial cartilages and ligaments. Consequently, monophyly of *Embolichthys* or *Bleekeria* is not supported by data because *Bleekeria viridianguilla* appears more closely related to *Embolichthys mitsukurii* than *E. sarisa* is to *E. mitsukurii*. *Embolichthys sarisa*, characterized by scales with membranous cteni, is

sister species to *Bleekeria* (minus *B. viridianguilla*), *Hyperoplus*, *Gymnammodytes*, and *Ammodytes*. All those taxa are united by absence of teeth on premaxillary and dentary. Monophyly of *Bleekeria* (minus *B. viridianguilla*) is supported by a unique lepidology in which ventral lateral field overlaps the posterior field and this abbreviated *Bleekeria* becomes sistergroup to rest of Ammodytidae. Monophyly of *Ammodytes*, *Gymnammodytes* and *Hyperoplus* is substantiated by ventrolateral skin folds, anterior field radial ridges, modified caudal lateral line scale with perforated groove, smooth nasal organ, neural and hemal spines blade-like and wide, loss of premaxillo-rostral ligament and accessory labial cartilages. *Ammodytes* appears paraphyletic due primarily to plesiomorphic scale patterns on body of *Ammodytes tobianus* which becomes sister species to *Gymnammodytes*, *Hyperoplus* and residue of *Ammodytes*. That clade is not resolved by strong synapomorphies since monophyly of *Hyperoplus* - *Gymnammodytes* is supported by only one dubious character, round scales. Interrelationships of other *Ammodytes* species is partially resolved by shape of ultimate modified caudal lateral line scale. A new character coding scheme for scales is devised which divides scales into units of variation corresponding to their fields and within this context the phylogenetic significance of four field scales and greater than five anterior field scalelets are discussed.

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Introduction

Ammodytidae are a small family of marine fishes comprised of five genera and approximately twenty species. They are relatively small rarely exceeding 20 cm. in standard length. The name of the family was derived from the Greek words 'ammos' and 'dytes' which translate to sand and diver, respectively (Pietsch and Zebatian 1990). Large schools of ammodytids, especially in the genus *Ammodytes*, are found swimming over or buried in sandy substrates (Bigelow and Schroeder 1953, Bryant 1993). Ammodytids also exhibit an eel-like shape and swimming motion. Consequently, the common names, sand diver, sand lance or sand eel, are used for many species, especially in the genus *Ammodytes*.

During the day sand eels are observed with only their heads out of sand facing into the current, a behavior that has been postulated as enhancing both feeding and predator avoidance (Bryant 1993, Reay 1973, 1970, Meyer et al. 1979), although in some instances they are not always successful in averting predation (Bigelow and Schroeder 1953). Sand burrowing is also a form of winter hibernation (Winslade 1974, Dick and Warner 1982, Healy 1984, Quinn and Schneider 1991). Quinn and Schneider (1991) found that winter-acclimatized, sand-burrowing *Ammodytes hexapterus* maintained oxygen consumption rates, independent of ambient oxygen

partial pressure, at a lower critical ambient oxygen partial pressure than burrowing, summer-acclimatized fish. These observations, along with finding lowered respiratory rates for winter-acclimatized fish, are consistent with results found for other hibernating organisms. Sand diving might also be a form of prespawning behavior (Hashimoto and Kawasaki 1981) and Hashimoto (1991) speculated that burrowing in sand could concentrate spawning.

Studies in the North Atlantic have shown that sand lances are important trophic links in marine ecosystems. Species of *Ammodytes* are pelagic plankton and benthic invertebrate feeders (Bigelow and Schroeder 1953, Reay 1970, Richards 1982) and they are in turn key components in the diets of flounder, haddock, hake, cod, Atlantic salmon, whales (Bigelow and Schroeder 1953, Overholtz and Nicolas 1979, Payne *et al.* 1986, Nizinski *et al.* 1990) and sea birds (Reay 1970, Safina and Burger 1985). Commercial harvesting of *Ammodytes* for human consumption is a significant industry in the North Sea and Japan (Stevens *et al.* 1984, Reay 1986), but in North America they are rarely used for food (Bryant 1993). However, they have been (Bigelow and Schroeder 1953) and continue to be part of a significant industry supplying bait for hook and line angling.

The family contains eight nominal genera (Eschmeyer 1990): *Ammodytes* (Linnaeus 1758b), *Ammodytoides* (Duncker and Möhr 1939, Ida and Randall 1993), *Argyrotaenia* (Gill 1861),

Bleekeria (Günther 1862), *Embolichthys* (Jordan and Evermann in Jordan 1903), *Gymnamodytes* (Duncker and Möhr 1935), *Herklotsina* (Fowler 1931) and *Hyperoplus* (Günther 1862). The following list includes genera and species currently recognized as valid. The first species listed under the bold generic name is the type species. References in parentheses after the generic name are authors who recognize validity of the genus.

***Ammodytes* Linnaeus (1758)**, (Wheeler 1973, Steven et al. 1984, Ida in Masuda 1984, Reay in Whitehead et al. 1986, Winters and Dalley 1988);

Ammodytes tobianus (Linnaeus 1758).

Ammodytes hexapterus (Pallas 1811).

Ammodytes personatus (Girard 1857).

Ammodytes americanus (Dekay 1842).

Ammodytes dubius (Reinhardt 1838).

Ammodytes marinus (Raitt 1934).

***Bleekeria* Günther (1862)**, (Stevens et al. 1984 Heemstra 1986);

Bleekeria kallolepis (Günther 1862).

Bleekeria vagus (McCulloch and Waite 1916).

Bleekeria gilli (Bean 1895).

Bleekeria renniei (Smith 1957).

Bleekeria viridianguilla (Fowler 1931)

***Ammodytoides* Duncker and Mohr (1939)**, (Ida and Randall 1993);

Ammodytoides vagus (Duncker and Mohr 1939)

Ammodytoides kimurai (Ida and Randall 1993)

***Embolichthys* Jordan (1903)**, (Steven *et al.* 1984, Ida 1984);

Embolichtys mitsukurii (Jordan and Evermann 1903).

Embolichthys sarisa (Robins and Böhlke 1970).

***Gymnammodytes* Duncker and Mohr (1935)**, (Wheeler 1973, Heemstra 1986, Stevens *et al.* 1984, Reay in Whitehead *et al.* 1986);

Gymnammodytes semisquamatus (Jourdain 1879).

Gymnammodytes cicereus (Rafinesque 1810).

Gymnammodytes capensis (Barnard 1927).

***Hyperoplus* Günther (1862)**, (Wheeler 1973, Stevens *et al.* 1984, Reay in Whitehead *et al.* 1986);

Hyperoplus lanceolatus (LeSauvage 1924).

Hyperoplus immaculatus (Corbin 1950).

Ammodytidae have a wide marine distribution in littoral and neritic waters. All six species of *Ammodytes* occur north of the equator in Atlantic and Pacific oceans. *Ammodytes hexapterus* was considered amphiboreal or

circumpolar (Walters 1955, Andriyashev 1954, McAllister 1960, Richards et al. 1963) but is generally regarded with *A. personatus* as having a north Pacific distribution (Hashimoto 1991, Okamoto 1989, Okamoto et al. 1989, Okamoto et al. 1988, Hashimoto 1984, Kobayashi 1961). *Ammodytes americanus* and *A. dubius* are confined to northwest Atlantic (Nizinski et al. 1990, Richards et al. 1963). *Ammodytes marinus* and *A. tobianus* occur in the northeast Atlantic along with *Hyperoplus lanceolatus*, *H. immaculatus* and *Gymnammodytes semisquamatus* (Raitt 1934, Einarsson 1951, Andriyashev 1954, Reay 1970, Winters and Dalley 1988, Sabatés et al. 1990, Hashimoto 1991). *Gymnammodytes cicerelus* is endemic to the Mediterranean (Sabatés et al. 1990). Species of *Gymnammodytes* have a bipolar distribution, with *G. cicerelus* and *G. semisquamatus* found in Mediterranean or off coasts of Europe and *Gymnammodytes capensis* located in South African waters (Einarsson 1951, Andriyashev 1954, Reay 1970, Heemstra 1986, Sabatés et al. 1990).

With exception of *Embolichthys sarisa* (Robins and Böhlke 1970), which is known only from the Caribbean, all 5 species of *Bleekeria* and *Embolichthys mitsukurii* are found in tropical and subtropical Indo-Pacific seas (Günther 1862, Bean 1895, McCulloch and Waite 1916, Fowler 1931, Smith 1957, Stevens et al. 1984, Heemstra 1986). Interestingly, no additional individuals of *E. sarisa* nor any other

ammodytids have been reported from tropical latitudes of the Atlantic since *E. sarisa* was first described.

Monophyly of Ammodytidae is well supported by these synapomorphies from Pietsch and Zebatian (1990):

1. Complex association of extra cartilages and ossicle in jaw (Gosline 1963, Ida 1976).
2. Anteriorly directed symphyseal process on dentary.
3. Large oval-shaped foramen in dentary.
4. Spine-like, dorsally directed process on lateral surface of metapterygoid.

In addition to those characters, many ammodytids share these attributes (Gosline 1963):

1. Infraorbital bones incomplete with lacrimal and second infraorbital separated from the rest of the series.
2. Caudal forked or emarginate, preceded by a well marked caudal peduncle that is supported by five or more vertebrae with blade like neural and hemal spines. Vertebrae 55-69, with abdominal more numerous than caudal.
4. Dorsal and anal rays have an approximately one to one relationship with corresponding vertebrae.
5. Cleithrum and supracleithrum almost vertically aligned.


Other characters commonly used to distinguish the family include: elongate body, protrusile premaxillaries, no fin spines or unsegmented rays except for procurrent rays of caudal fin, pelvic fins highly reduced or absent and sand-burrowing behavior (Gosline 1963, Reay 1970, Lauder and Liem 1983, Pietsche and Zebatian 1990).

Ammodytidae have been considered part of Perciformes, an order within Acanthomorpha (Gosline 1963, Nelson 1984, Pietsch and Zebatian 1990) but phylogenetic position of the family within this taxon has been somewhat obscured by lack of resolution and homoplasy in higher level acanthomorph relationships (Johnson and Patterson 1993). Position of Ammodytidae in Perciformes is confounded by the possibility that perciforms are polyphyletic (Patterson 1964, Greenwood *et al.* 1966, Rosen 1973). While some progress has been made in defining the group, most investigators could find no synapomorphies for the order (Greenwood *et al.* 1966, Rosen 1973, Lauder and Liem 1983, Johnson 1993, Rosen and Patterson 1990, Johnson and Patterson 1993) although recently Roberts (1993) believed transformed ctenoid scales is one.

Few groups have had as much diversity of opinion regarding their relationships to other fishes as the Ammodytidae. Lack of obvious affinity to any known teleostean groups has caused ammodytids to be placed in widely different relational schemes, such as coryphaenids (Artedi 1738, Swainson 1839), gadiforms (Cuvier 1816, Bleeker 1859), atherinomorphs (Gill 1861, 1862a) and herrings (Kyle 1923). The most detailed phylogenetic work so far (Pietsch and Zebatian 1990) has Ammodytidae positioned within trachinoids, a hypothesis first proposed by Gill (1904). Pietsch and Zebatian (1990) believed they

are the sister group to Uranoscopidae and Trachinidae. However, these results were primarily based upon a study of only one ammodytid species, the phylogenetically most primitive, *Embolichthys mitsukurii*. Epidermal covering united between scales, scales in oblique rows and scales at right angle to oblique rows were utilized as synapomorphies for ammodytids, uranoscopids and trachinids but these specializations only occur in *Ammodytes* and *Hyperoplus* not *Embolichthys mitsukurii*, *Bleekeria* or *Gymnammodytes*. Thus, Pietsch and Zebatian (1990) used a synthetic ammodytid as representative of the family and inclusion of all ammodytid genera in their data matrix, with accurate character coding, profoundly affects resolution of their tree (Fig. 2b).

External patterns of ridges and grooves on ammodytid scales are distinctive and perhaps placement of Ammodytidae in some tenable phylogeny might be simplified by locating taxa with similar scales. Most systematic efforts dismissed their scales as being simply cycloid (Jordan 1906, Reay 1970, Nelson 1984, Pietsch and Zebatian 1990), except Günther's (1862) description of scales from *Bleekeria kallolepis*. He found the posterior margin finely lobate or tooth-like, scale surface furrowed by concentric and radiating striae and where striae crossed a small nodule is produced. Gill (1904) pictured scales of *Ammodytes tobianus* and *Hyperoplus lanceolatus* but did not comment on significance of their similarity or uniqueness in a wider

phylogenetic context. Jordan (1906) reported that scales of *Embolichthys* are sculptured but mentioned nothing more. Two papers contained photographs of *Ammodytes* scales (Kändler 1941, Pietsch and Zebatian 1990), illustrating abundant morphological detail but they did not break with tradition and continued to describe their scales as cycloid. 

Ammodytidae demonstrate scale diversity is a source of phylogenetic information which has been camouflaged under the two great paradigms of teleostean lepidology, 'cycloid' and 'ctenoid'. Older ichthyological texts (Agassiz 1877, Günther 1880, Benecke 1881, Goodrich 1909) as well as shorter monographs (Cockerell 1911, 1913, Chu 1935, Lagler 1947) illustrated and gave numerous examples of scale variation but most systematic or classification schemes dealing with euteleosteans (Rosen 1973, 1985, Lauder and Leim 1983, Nelson 1984) relied on traditional cycloid or ctenoid descriptions. Such interpretation of scale variation virtually eliminated the impact of actual diversity on euteleostean phylogenetic schemes. Exceptions exist in the work of Lagler (1947), McCully (1961) and Roberts (1993), who discussed and used the abundant phylogenetic information contained in scale morphology. Other work has uncovered the systematic value of detailed scale morphologies in less inclusive groups (Delamater and Courtenay 1973a, 1973b, 1974, Hughes 1981, Liu and Shen 1991, Coburn and Gaglione 1992) but only Coburn and Gaglione

(1992) coded variation into character data for purpose of phylogenetic inference.

The problem of calling ammodytid scales cycloid, is essentially a question concerning homology. Is the lepidology of *Parasudis* (Fig. 29) homologous to the patterns on scales of *Embolichthys mitsukurii* (Fig. 12)? Scales from *Parasudas* are comprised of only concentric ridges and those of *Embolichthys mitsukurii* reveal four fields with anterior scalelets and posterior radial ridges. There are obviously many differences between the two and using the term cycloid for both scales ignores their dissimilarity. Therefore, employment of the term cycloid for a more complex lepidology, such as one finds in Ammodytidae, is as Nelson (1978, p. 344) has said '...an indication that the characters and transformations are merely poorly understood and, consequently wrongly defined.'

Occurrences of cycloid scales in Percomorpha are relatively common and have been described as homoplasious reversals from the plesiomorphic ctenoid condition (Johnson 1984) but in fact many so-called cycloid scales share many features in common with ctenoid scales. These lepidologies include: scale divided into four uniquely patterned areas or fields, anterior field scalelets and pentagonal shape. Such observations strongly suggest reevaluation of current notions concerning definitions of 'cycloid' scales, in a similar manner to Roberts' (1993) work with ctenoid scales.

The term ctenoid covers a highly diverse group of scales (Johnson 1984, Roberts 1993) but Roberts redefined ctenoid scales placing them into different categories based upon actual morphology of spines or cteni. Transformed ctenoid scales characterized one of his groupings and was used as the sole synapomorphy for Perciformes (Roberts 1993). Johnson and Patterson (1993) utilized transformed ctenoid scales in a somewhat wider phylogenetic framework, when they employed it as one of several synapomorphies for Percomorpha.

Reanalysis of acanthomorph and ammodytid scale morphology is done here with special emphasis on those designated cycloid. Traditional concepts of 'cycloid' and 'ctenoid' are replaced by a scheme which recognizes regions on the scale plate or fields as sources of character data. These fields are roughly triangular wedges whose boundaries converge on the central focus and divide the scale into four sections or fields; **anterior**, **posterior** and two **lateral**. These fields are named for their orientation on the scale relative to scale orientation on the fish. Thus, the terms *anterior* and *posterior* are used for two fields whose position on scales corresponds with a fishes anatomical anterior and posterior directions. Lateral is not the anatomical lateral but rather the dorsal or ventral sections of the scale relative to the scale's and fish's anterior-posterior longitudinal axis.

Characters from these fields more accurately portray scale diversity and demonstrate that scale characters can greatly influence phylogenetic analyses. For example, Coburn and Gaglione (1992) showed structure of cteni from posterior scale fields distinguish percids from moronids, centrarchids and percichthyids. They also integrated their scale character data with other morphological characters in a parsimony analysis of percids. Their work is an excellent example of cumulative tabulation of character data derived from different sources, a process advocated by Johnson (1984) for future phylogenetic analysis of large problematic groups such as Perciformes. In a similar manner, scale character data is integrated with characters derived from investigations of osteology, myology and external anatomy in order to formulate a phylogenetic hypothesis for species of Ammodytidae.

Historical Review of Ammodytidae Systematics

The earliest systematic record of ammodytids was Artedi (1738) who recognized the genus *Ammodytes* and placed it next to *Coryphaena*. Continuous dorsal fin without spines was the basis for Artedi (1738, 1962 reprint) and later Swainson (1839) postulating an affinity with coryphaenids. An eel-like shape, continuous dorsal fin without spines and lack of pelvic fins on then known species of *Ammodytes* were obvious reasons for early placement of ammodytids near or in the ophidiids (Risso 1810, Cuvier 1816, Bonaparte 1846, Bleeker 1859, Günther 1862, Gill 1884, 1893). Bonaparte (1846) actually was the first investigator to separate *Ammodytes* from the family of ophidiids. A partial synonymy of the family names for Ammodytidae by Gill (1904) also indicated that Bonaparte (1846) was probably the first to recognize the family name.

Gill (1861) was the earliest to establish a closer association of ammodytids with atheriniforms, because of similarity in the structure of the jaw (Pietsch and Zebatian 1990), when he removed them from association with ophidiids and placed Ammodytoidea after Atherinoidea in suborder Physoclysti. The appellation, Ammodytoidea, followed the convention promoted by Agassiz, who felt all family names derived from Greek words should end in -oidea (Gill 1904).

Physoclysti are fishes without a connection between the swim bladder and intestinal canal. They correspond to acanthopterygians recognized in more recent literature (Rosen 1973, Johnson and Patterson 1993). Inclusion of Ammodytidae in this larger assemblage was somewhat problematic considering they do not have swim bladders. Later Gill (1962), discontinued use of the Physoclysti as a taxonomic unit and placed Ammodytidae in Anacanthini, Incertae Sedis, of Teleocephali. He changed his mind again when he (Gill 1873) described ammodytids as an incertae sedis super-family situated between suborders Acanthopteri and Percosoces (Gill 1873). Percosoces generally contains mugilids, atherinids, sphyraenids (Jordan and Gilbert 1882) and scombresocids (Boulenger 1904a).

Late in the nineteenth and early twentieth century Ammodytidae were placed near Percosoces (Jordan and Evermann 1896, Woodward 1901, Jordan 1903 and Boulenger 1904a). Woodward (1901) postulated an ammodytid affinity to the extinct Oligocene *Cobitopsis* Pomel. *Cobitopsis* had been included in Percosoces, between the extinct Crossognathidae and extant, Scomberesocidae (Gill 1904), but today is placed in Hemiramphidae (Pietsch and Zabetian 1990). Virtually no anatomical evidence was presented with this hypothesis, except for a restored illustration of the fossil *Cobitopsis*, which was originally drawn by Gervais (1848-1852). It is difficult to understand how this hypothesis of a ammodytid-

Cobitopsis relationship evolved but perhaps Woodward relied on overall similarity of *Cobitopsis* to the former ammodytid, *Hypoptychus*, which possesses a similar posterior positioning of dorsal and anal fins. The shortcoming of this hypothesis was apparent years later when it became increasingly obvious that *Hypoptychus* was not an ammodytid (Gosline 1967, Ida 1976).

Hypoptychus dybowskii was originally placed in Ammodytidae by Steindachner (1880). However, Ida removed the species in 1976 because of convincing evidence which placed *Hypoptychus* with gasterosteiforms. Additional evidence with regard to morphology of nasal organ (Theisen 1984) seemed to support the placement. However, inclusion of *Hypoptychus* in the gasterosteiforms is problematic (Johnson and Patterson 1993). With *Hypoptychus* in the group there is scant evidence for monophyly of the gasterosteiforms, not to mention additional conflicts associated with inclusion of Aulorhynchidae and Syngnathoidei in the order. Nevertheless, *Hypoptychus* appears to be more closely related to *Aulichthys* than ammodytids or other gasterosteiforms (Johnson and Patterson 1993).

The turning point in ammodytid systematic was the discovery of jugular pelvic fins on a tropical Pacific ammodytid, originally described as *Bleekeria mitsukurii* by Jordan and Evermann (1902) and moved to *Embolichthys* by

Jordan (1903). Jordan (1903) felt that jugular pelvics of *Embolichthys* challenged the relationship to *Percesoces* or the extinct percesocoid, *Cobitopsis*. In 1905 he completely excluded Ammodytidae from *Percesoces* which signaled the end for serious considerations of an Ammodytidae-*Percesoces* relationship.

The hypothesis of trachinoid affinity (Pietsch and Zabetian 1990) is central in current discussions of ammodytid phylogeny (Johnson 1993). The hypothesis was first suggested by Gill (1904) when he saw a resemblance between ammodytids and the percophiid, *Hemerocoetes*. Despite Gill's (1904) belief in a relationship to *Percesoces*, he discussed how ammodytids reminded him of the New Zealand percophid, *Hemerocoetes*, based upon simple articulated dorsal rays. Gill (1904) also inferred a trichonotid-ammodytid affinity by mentioning the possible association of *Hemerocoetes* and *Trichonotus* [*Trichonotus* is a member of trachinoid family Trichonotidae (Nelson 1984, 1986)]. Regan (1913) briefly discussed the relationship of *Cobitopsis* to ammodytids and extant scombresocids but concluded that the closest relative of ammodytids may be percophids. Unlike Boulenger (1904b), who felt only two ammodytid genera, *Bleekeria* and *Embolichthys*, were relevant to this relationship, Regan included *Ammodytes*, *Bleekeria*, *Hyperoplus*, *Embolichthys* and *Hypoptychus* in his hypothesis. Jordon (1923) also implied a relationship to Trichonotidae

(Family 571) which were contained in Percophidiformes when he positioned the ammodytiform families: Ammodytidae (family 573), Bleekeridae (family 574) and Hypoptychidae (family 575), between Bathymasteriformes and Percophidiformes. Pietsch and Zabetian's (1990, fig. 2a) trachinoid-ammodytid phylogeny placed Ammodytidae as sister group to a monophyletic Uranoscopidae plus Trachinidae and had Leptoscopidae as sister group to these three families. They also had a monophyletic Trichonotidae, Creediidae and Percophidae as sister group to a fully resolved clade comprised of Chamsodontidae plus Chiasmodontidae, Leptoscopidae, Ammodytidae and Trachinidae plus Uranoscopidae (Fig. 2a).

In a radical departure from accepted paradigms of teleostean systematics, Kyle (1923) questioned the assumed primitiveness of berycoids as ancestors to percoids when he postulated a group termed Teleostei Anteriores. This new group was divided into five orders, Irregulares, Trachinoidea, Carangoidea, Percoidea and Scombroidea based upon what he termed "... balancing conditions of the abdominal region." (p. 203). By balancing conditions, he used a suite or combination of characters which included: forward growth of anal interradiania or anal pterygiophores, anterior anal interradiania represented by a stout bone or abdominal rod, nature of urohyal attachment to branchial arches and osteology of vertebral zygapophyses. He then

attempted to find a generalized form from which these orders were derived and concluded that it was *Ammodytes*. Kyle (1923, p.235) further concluded that *Ammodytes* "is a variant of the Herring." This conclusion was based upon similarities of larval forms, mid caudal vertebrae and the higher ratio of abdominal to caudal vertebrae. Kyle's hypotheses were never seriously considered, especially the ammodytid-herring alignment. His hypotheses illustrate the shortcoming of using symplesiomorphy as a criteria for inferring relationships. He did demonstrate however, that ammodytids are more primitive in some respects to other putative members of Perciformes, an assemblage in which ammodytids are assumed to belong (Gosline 1963, Greenwood et al. 1966, Gosline 1968, Lauder and Liem 1983, Nelson 1984).

The fossil record of ammodytids is limited to otoliths and sheds little light on their phylogenetic position. Earliest otoliths are from the Eocene shell sands of Brittany (Nolf 1978). Oligocene deposits that yield fossil ammodytid otoliths include Astrup, Germany (Menzel 1980), Kasseler Sea Sands (Menzel 1983) and Bassevelde Sand of Ruisbroek, Belgium (Gaemers 1984). Deposits from Antwerp, Belgium (Nolf 1978, Gaemers and Schwarhans 1973) and Ouwerkerk, Netherlands (Gaemers and Schwarhans 1973) bear Pliocene-Pleistocene otoliths. Fossilization of Ammodytidae are similar to Cretaceous percoids (Patterson 1993), in that there are only otoliths and no skeletal remains. Aside from

this parallel pattern of fossilization, fossil otoliths do not contribute any additional phylogenetic information which has already been obtained from extant otoliths (Nolf 1993). Nolf (1993) believed that otolith morphology corroborated the hypothesis of an ammodytid-trachinoid relationship.

Atlantic *Ammodytes*

Intrarelationships within the genus *Ammodytes* is the most ambiguous aspect of ammodytid phylogeny due to a high degree of similarity between species. The tradition of using meristic characters to separate *Ammodytes* species has generated abundant taxonomic confusion due to the great variability and wide overlap of these characters. Much of this overlap and variability is probably the result of environmental factors, such as temperature or salinity (Richards *et al.* 1963, Einarsson 1951, 1955, Andriashev 1954, Berg *et al.* 1949, Perlmutter 1940, Bruun, 1941, Jensen, 1941, 1944, Kändler, 1937).

Jensen (1941, 1944) discussed impact of water temperature on *Ammodytes*, noting higher number of meristic counts in specimens obtained from colder waters. Jensen (1944) showed that lower water temperatures during early development correlates with higher vertebral and median fin ray counts but that latitudinal variation is only a factor if it covaries with temperature. Clinal meristic variation

of *Ammodytes* confirms the effect of water temperature on meristics as well (Winters and Dalley 1988, Richards 1963, 1982, Nizinski et al. 1990). Influence of water temperature on body shape was suggested in species descriptions of Reinhardt (1838), Günther (1862) and Jordan and Gilbert (1882). They all characterized a northern species, *A. dubius*, with slender, long bodies and high meristic counts. Perlmutter (1940) and Richards et al. (1963) also found that body depth of an intermediate-high meristic count northern group was less than a low-intermediate count southern group. Nonetheless, none of these studies demonstrated that environmentally induced variability was implicated in misidentification or spurious recognition of species.

Collette (per. com.) listed 23 historical names for species of *Ammodytes* which demonstrate that species designations proliferate when based primarily upon meristics. I augment his list with subspecies to further illustrate this phenomena. Table 1 is a revised listing of species and subspecies originally placed or misplaced in the genus *Ammodytes*. Furthermore, Table 1 illustrates three systematic trends in the taxonomic history of the family.

The first trend occurred when species of *Ammodytes* were initially identified. The difficulty in characterizing them caused a proliferation of new species names. Later it became apparent that some of these fishes had obvious and unique anatomical characteristics distinguishing them from

Ammodytes. *Ammodytes lanceolatus* was removed to *Hyperoplus* by Günther (1862) because it possessed fanged vomers (*Ammodytes* lack fangs). *Ammodytes immaculatus*, originally described by Corbin (1950), belonged in *Hyperoplus* because it also has fanged vomers (Reay 1986). *Ammodytes cicereus* was placed in *Gymnammodytes* (Duncker and Möhr 1935) because the anterior half of its body has no scales, while species of *Ammodytes* have bodies covered completely by oblique scale rows. *Ammodytes lucasanus* (Beebe and Tee-Van 1938) lacks oblique scale rows and ventro-lateral skin folds, which are highly characteristic of *Ammodytes*, and was later found to be junior synonym of *Bleekeria gilli* (Collete MS, Duncker and Möhr 1939).

The second systematic trend from the 1930's to the 1950's was characterized by a proliferation of subspecies appellations (Kändler 1937, Perlmutter 1940, Jensen 1941, Berg *et al.* 1949, Einarsson 1951, Andriyashev 1954), apparently done to resolve the systematic confusion. However, the ineffectiveness of subspecies in solving the taxonomic confusion is demonstrated by their complete disregard as taxonomic units in later investigations (Richards *et al.* 1963, Richards 1982, Winters and Dalley 1988, Okamoto 1989, Nizinski *et al.* 1990, Hashimoto 1991).

The final historical phase, from the early 1960's to the present, is distinguished by more sophisticated statistical analyses and utilization of increasingly larger

data bases of meristics to differentiate species. Nizinski *et al.* (1990), Richards *et al.* (1963), Richards (1982), Einarsson (1951) and Winters and Dalley (1988), found number of vertebrae a 'good' character for differentiating species of *Ammodytes*, but relatively large overlaps in vertebrae counts made complete resolution of species difficult. Richards *et al.* (1963) used confidence limits taken from the Student's *t* distribution and coefficients of difference. Winters and Dalley (1988) applied bivariate discriminant function analysis and modal analysis by computer. Hashimoto (1984) calculated Mahalanobis distance (1984) [a discriminant function method]. Nizinski *et al.* (1990) conducted principal component analyses using numbers of plicae, vertebrae, dorsal fin rays, anal fin rays, pectoral fin rays and gill rakers on first arch as data. These studies have shown that, despite close morphological similarities, there are subtle differences in meristics which have helped resolve some problems associated with recognizing *Ammodytes* species.

Jensen (1941), Einarsson (1951), Andriyashev (1954) Backus (1957), Reay (1970) and Richards *et al.* (1963) discussed problems associated with *Ammodytes* species nomenclature. Confusion essentially began with Linnaeus' designation of some specimens as *Ammodytes tobianus*. One of the specimens Linnaeus examined actually belonged to the later described species, *Ammodytes lanceolatus* (Lesauvage

1824), which was moved to *Hyperoplus* by Günther (1862). According to Jensen (1941), the specimen was not considered a type specimen by Linnaeus but despite that fact and the technicality that *Ammodytes lancea* is a junior synonym of *A. tobianus*, Jensen felt *A. lancea* (Cuvier 1829) should take precedent over *A. tobianus* because of Linnaeus' misidentification. On the other hand, Andriyashev (1954) argued for exclusive recognition of the senior synonym, *Ammodytes tobianus*, since it was the first valid name used for the species. He recognized the possibility that Linnaeus had mistakenly identified one of the original specimens but held that it was not important as long as the types were correctly identified. Andriyashev used *Ammodytes tobianus* to describe some of the sand lances in northern Soviet seas and held it in synonymy with *Ammodytes* of Artedi (1738, 1962 reprint), *Ammodytes tobianus* Linnaeus (1758), *Ammodytes lancea* Cuvier (1829) and *Ammodytes lancea lancea* Jensen (1941). Backus (1957), Richards et al. (1963) and Reay (1970) agreed with the opinions of Andriyashev (1954) and recognized *Ammodytes tobianus* as well. Consequently, *Ammodytes tobianus* is the accepted name of the lesser European sand lance (Reay 1970). *Ammodytes tobianus* is clearly different from all other species of *Ammodytes* because it has distinctive, diagnostic external anatomical features which reliably segregate it (Reay 1970). These characters are: scales over musculature at base of caudal

fin, scales on ventral surface in tight chevrons, scales on dorsal surface extend just anterior to and alongside dorsal fin. Post-larval pigmentation patterns (Einarsson 1951, 1955, Corbin and Vati 1949, Macer 1967, Richards 1982) also distinguished *A. tobianus* from other species of *Ammodytes*. The patterns of body scales on *A. tobianus* suggest it is the most plesiomorphic *Ammodytes* but its position in the genus has never been tested phylogenetically.

Reinhardt (1838) first described *Ammodytes dubius* from Greenland and segregated it from other European sand eels because of higher dorsal and anal fin ray counts. *Ammodytes dubius* has been widely recognized as a distinct species occurring off Greenland or in more northerly Arctic waters (Krøyer 1846-1853 and Vanhöffen 1891-1893, mentioned by Jensen 1941, Günther 1862, Jordan and Gilbert 1882, Vladykov 1933, Jensen 1941) and the northwestern Atlantic (Walters 1955, Backus 1957, McAllister 1960, Richards *et al.* 1963, Winters and Dalley 1988; Nizinski *et al.* 1990). Richards *et al.* (1963) and Winters and Dalley (1988) believed *A. dubius* occurred offshore in the northwest Atlantic from Cape Cod to Greenland. However, Winters and Dalley (1988) also described an inshore distribution from West Greenland to the Gulf of Maine. This was refuted by Nizinski *et al.* (1990) who effectively showed that *A. dubius* occurred predominantly offshore from North Carolina to Greenland.

DeKay (1842) described *Ammodytes americanus* from

specimens collected around New York but he had only four meristic values in his description [dorsal ray 56, anal fin rays 27, pectoral fin rays 13 and caudal rays 17]. These values along with an accurate but undistinguished description of external morphology left much room for interpretation of the species. Richards *et al.* (1963) apparently considered *Ammodytes americanus* synonymous with *A. hexapterus* when they used the latter name for an inshore circumpolar sand lance ranging from Labrador to Cape Cod in the northwest Atlantic. They presented no direct evidence for this synonymy but the use of *A. hexapterus* for any northwest Atlantic ammodytid never appeared again in the literature. Reay (1970) claimed that most authors after 1966 subscribed to the nomenclature of Leim and Scott (1966) who felt only *A. americanus* and *A. dubius* existed in the northwest Atlantic.

Nizinski *et al.* (1990) convincingly showed that *A. americanus* is primarily a shallow water coastal form and occurs inshore from Labrador to southern Delaware. Nizinski's *et al.* (1990) conclusions basically corroborate Richard's *et al.* (1963) and both disagreed with Winters and Dalley (1988), who believed there was an offshore population of *A. americanus* from Georges Banks southward.

Sympatry of *Ammodytes dubius* and *Ammodytes americanus* in Newfoundland waters was recorded by Winters and Dalley (1988) but according to Richards *et al.* (1963), sympatry of

the two species only occurs from the Labrador coast northward and offshore south of Cape Cod during the first summer of growth for *A. americanus*. In their definitive study Nizinski et al. (1990) clearly separated the species into two groups but reported co-occurrence of *A. dubius* and *A. americanus* in limited inshore coastal areas.

Nevertheless, these two species basically segregate into a coastal *A. americanus* and offshore *A. dubius*. The straightforward method (Nizinski et al. 1990) of simply counting plicae reliably divided the two species at a boundary of 124 and 125 plicae, 98.8% of the time. In addition, plots of plicae vs number of vertebrae produced 100% separation over the entire geographical range.

The European offshore *Ammodytes marinus*, was characterized by Raitt (1934), who considered it a distinct species and separate from *A. tobianus*. Duncker and Möhr (1939), in their revision of the Ammodytidae synonymized *A. marinus* and *A. hexapterus*. Others have, combined *A. marinus*, *A. hexapterus* and *A. americanus* (McAllister 1960), believed they are a circumpolar complex (Walters 1955) or felt *A. marinus* and *A. americanus* are a single trans-Atlantic species (Winters and Dalley 1988). Resemblances of post-larval pigmentation between *A. marinus* and northwest Atlantic *A. americanus* and *A. dubius* (Richards 1982, Macer 1967) and temporal similarity of spawning seasons and occurrence of larvae imply a connection between *A. marinus*

and northwest Atlantic sand eels (Walters 1955). However, other data (Richards *et al.* 1963, Nizinski *et al.* 1990) including presence of an extra hyomandibular spine on some specimens of *A. marinus* (Fig. 129) argue against such a relationship.

Winters and Dalley's (1988) proposal of a trans-Atlantic *Ammodytes marinus* was based on the assumption that inshore northwest Atlantic Greenland specimens were *A. americanus*. Additional evidence was presented to substantiate their hypothesis which included wide overlap in meristic counts of *A. marinus* and *A. americanus* and the following similarities: patterns of north-south meristic clines, amounts of latitudinal meristic variation and inshore-offshore body shape changes. Two populations at the same latitude on opposite sides of the Atlantic showing similar meristic and body form variation is hardly enough evidence, upon which to base a trans-Atlantic *A. marinus*. Plus, it is doubtful that *A. americanus* is found offshore or inshore at a latitude greater than 60°N (Richards *et al.* 1963, Nizinski *et al.*, 1990). Consequently, Winters and Dalley's (1988) proposal is not well substantiated but the trans-Atlantic relationships of *A. marinus*, *A. dubius* and *A. americanus* remain to be elucidated.

Pacific *Ammodytes*

Five species of northern Pacific sand lances have been recognized: *Ammodytes personatus* Girard (1857), *A. hexapterus* Pallas (1811), *A. japonicus* Duncker and Möhr (1939), *A. alëutensis* Duncker and Möhr (1939) and *A. alascanus* Cope (1873) (Jordan and Gilbert 1899, Jordan 1906, Lindberg 1937, Perlmutter 1940). Relationships of these forms to each other and to Atlantic *Ammodytes* are obscure. Günther (1862) recognized the European *A. tobianus*, the American *A. americanus* and the north Pacific *A. personatus* as distinct species but Jordan and Gilbert (1882), Dannevig (1918), Perlmutter (1940) and Bigelow and Schroeder (1953) believed that they are the same species. Scofield (1899) collected specimens from Arctic Alaska and compared them to others taken from Cape Flattery, Washington, the type locality of *Ammodytes personatus* (Girard) and felt that all these specimens, plus *A. alascanus* and the European *A. tobianus* were identical. Jordan and Gilbert (1899) counted dorsal and anal fin rays and oblique scale rows from specimens taken around Alaska noting agreement with the type for *A. alascanus* (Cope) but they also recognized their close similarity to Puget Sound *Ammodytes personatus* (Girard). Jordan (1906) identified a sand lance from Japan as *Ammodytes personatus* and described its range as an arc

starting from Japan, going north to Siberia, over to Alaska and south to Monterey Bay, California. He discussed lack of differences between European *Ammodytes tobianus*, Atlantic Coast *Ammodytes americanus*, Aleutian Islands *Ammodytes alascanus* and transpacific populations of *Ammodytes personatus* but also found Japanese *A. personatus* have greater number of plicae than European *A. tobianus*.

McAllister (1960) believed *A. marinus* and *A. americanus* are the same species yet he felt *A. personatus* is distinct.

Clemens and Wilby (1961) did not recognize *A. personatus* in Canadian Pacific waters but instead characterized all Canadian Pacific sand eels as *A. hexapterus*. Besides the original descriptions by Duncker and Möhr (1939) for *Ammodytes japonicus* and *A. alëutensis*, there has been no corroboration of their reality from other investigations.

Japanese literature on *Ammodytes* is especially extensive with many detailed papers containing meristic analyses of Japanese populations (Hatanaka and Okamoto 1950, Andriyashev 1954, Kobayashi 1961, Kitaguchi 1978, Hashimoto and Kawasaki 1981, Hashimoto 1984, Hashimoto 1991). Isozyme data has complemented the meristic data and definitive distributional patterns have emerged (Okamoto *et al.* 1988, Okamoto *et al.* 1989, Okamoto 1989, Hashimoto 1991).

Interestingly, Japanese ichthyologists have arrived at a greater consensual understanding of population structures around Japan than their western counterparts in the Atlantic

or Pacific, perhaps partly due to their use of corroborative isozyme evidence.

After Jordan (1906) identified *Ammodytes personatus* in Japanese waters most like Ohshima (1950) considered *A. personatus* to be the only Japanese sand lance. Hatanaka and Okamoto (1950) were among the first to investigate populations in Japanese waters and recognized subpopulations of *Ammodytes personatus*. In 1957, Ishigaki and Kaga studied distributions of *A. personatus* around Hokkaido and found a decrease in meristics from north to south. While they concluded that the sandlances of Hokkaido belong to the same species, they characterized subpopulations or local varieties.

Lindberg (1937) was the first to recognize two species of *Ammodytes* in Japanese waters, *A. personatus* and *A. hexapterus* but not until almost 50 years later was this confirmed. Kitaguchi (1979), Hashimoto (1984 1991) and Okamoto (1989) found a high vertebral mode population in the seas east of Cape Soya, northern Hokkaido, which they called *A. hexapterus*. Okamoto (1989) discovered two sympatric and genetically distinct populations of sand lances east of Cape Soya off northeastern Hokkaido, which he labeled *A. personatus* and *A. hexapterus*. *Ammodytes hexapterus* is fixed at four different alleles from the co-occurring *A. personatus* (Okamoto et al. 1988, Hatanaka and Kawasaki 1980). Later the subpopulation of *A. hexapterus* off

northern Hokkaido, east of Wakkanai, was characterized further with the α -Gpdh^s allele (Hashimoto 1991). These genetically distinct populations of *A. personatus* and *A. hexapterus* are probably reproductively isolated due to a three month difference in the peaks of their spawning periods (Okamoto 1989).

Data of Hashimoto and Kawasaki (1980, 1981), Okamoto et al. (1988) and Hashimoto (1984, 1991) characterized two additional subpopulations of *A. personatus* distributed around Japan. One northern subpopulation was located from southern Hokkaido to Sendai Bay on the Pacific side and to Tottori Prefecture on the Sea of Japan side. Another ranged around southern Japan, being sympatric with the first group in Sendai Bay and off the Tottori Prefecture (Hashimoto 1991, Hashimoto and Kawasaki 1981). The Pacific coast between the Miyagi and Iwate Prefectures is a boundary for these two populations of *Ammodytes personatus* (Hashimoto and Kawasaki 1981, Okamoto et al. 1988). Okamoto et al. (1988) also felt some gene flow occurs between subpopulations because the northern and southern groups share at least one allele out of ten on the loci surveyed.

Hashimoto and Kawasaki (1980) found that one subpopulations of *A. personatus* in and around Sendai Bay with a notched otolith [lower vertebral counts and no α -Gpdh^f allele], tended to have a more southerly distribution than another sympatric subpopulation with an arrowhead type

otolith [higher vertebral counts and an α -Gpdh^f frequency of .3]. Otolith structural variation may be due to differences in the breeding times of subpopulations (Kandler 1941, Jensen 1944). However, Kändler (1941) found no variation as great as that corresponding to an arrowhead versus notched otolith.

Kobayashi (1961) examined over 1600 larvae and young of *A. hexapterus* that were collected in an arc from the Okhotsk Sea over to Aleutian Islands and Bering Sea. These specimens have a higher number of vertebrae, as compared to populations of a more southerly, Japanese distribution. Kobayashi's meristic data were consistent with those of the type for *Ammodytes hexapterus* (Pallas 1811). The lower average, vertebral numbers from the Okhotsk Sea were also consistent with counts from specimens around Japan characterized as *A. hexapterus* by Okamoto (1989), Hashimoto (1984) and Hashimoto (1991). Thus, there is reason to believe that *A. hexapterus* is distributed across the northern Pacific. However, isozyme data challenges this assumption (Okamoto 1989).

Okamoto (1989) discovered that individuals collected from Kodiak Island had similar vertebral counts but a different genetic structure than the *A. hexapterus* from Japanese waters, the group east of Cape Soya. He used genetic distance (Nei 1972) to compare subpopulations in the north Pacific and found that genetic distance of Kodiak,

Alaska and east of Cape Soya *A. hexapterus* was approximately equal to genetic distance between Cape Soya *A. hexapterus* and northern or southern Japanese subpopulations of *A. personatus*. Thus, genetic distance could have indicated a different species was collected off Alaska. However, reliability of genetic distance values as comparative indicators of species is highly suspect. Genetic distance varies for different groups of organisms and it has not been shown to consistently reveal species boundaries based upon some particular magnitude (Shaklee et al. 1982). Therefore, in some cases genetic distance may only be showing population structure since it is difficult to assess what values one uses to distinguish among conspecific or congeneric populations of fishes.

Hyperoplus and *Gymnamodytes*

Günther (1862) originally described the genus *Hyperoplus* on the basis of two large fang-like teeth on the anterior end of the vomer. Gill (1904, figs. 3&4) and Kayser (1961, fig. 19) found *A. lanceolatus* (= *Hyperoplus lanceolatus*) has less protrusile premaxillaries with a more rigid and shorter premaxillary ascending process (Kayser, 1961, fig. 8) than *Ammodytes tobianus*. Ehrenbaum (1904, 1909) and Einarsson (1951, fig. 6 & 7, pp. 24 & 25) characterized post-larval *H. lanceolatus* by an anterior

notch on the vomer, a row of black chromatophores from the head to base of caudal fin and Macer (1967), Fage (1918), Kändler (1941), Corbin and Vati (1949), Einarsson (1951, 1955), Cameron (1959) and Richards (1965) made note of heavy post-larval pigmentation. The second species in the genus, *Hyperoplus immaculatus* can be separated from *Hyperoplus lanceolatus* by morphology of its vomerine tooth cusps, higher dorsal fin ray and vertebral counts and pigmentation on snout and lower jaw (Corbin 1950, Reay 1986, fig. 5, p. 945).

The systematic position of *Hyperoplus* within Ammodytidae is unresolved. However, a relationship with *Gymnammodytes* is suggested by the common occurrence of post-larval vomerine teeth. *Hyperoplus* and *Gymnammodytes* have vomerine teeth but they are lost in adults of *Gymnammodytes*. Homology of these vomerine teeth is questionable however, due to their vomers having a different shape. The post-larval vomer of *Gymnammodytes* has a slightly pointed anterior margin with two anterolateral pointed teeth while *Hyperoplus* shows a notched anterior margin formed by the fang-like teeth (Einarsson 1951, fig. 6 & 7).

Duncker and Möhr (1935 1939) described the genus *Gymnammodytes* and placed three species in it: *G. cicerelus* (Rafinesque 1810), *G. semisquamatus* (Jourdain 1879) and *G. capensis* (Barnard 1927). It was chiefly distinguished from other ammodytids by loss of body scales and scaleless

lateral line comprised of horizontal and vertical tubules. Occurrence of *Gymnammodytes capensis* (Barnard 1927) off South Africa is biogeographical interesting since the other species have a Mediterranean (*G. cicereus*) or Mediterranean-Northeast Atlantic (*G. semisquamatus*) distribution. Unfortunately, absence of systematic hypotheses for species of *Gymnammodytes* and intrarelationships with other ammodytids has made the bipolarity of *Gymnammodytes* a curious feature of the genus much like the characters which define it.

Gymnammodytes cicereus is endemic to the Mediterranean (Sabatés et al. 1990) but the first sand eels described there were called *Ammodytes tobianus* (Delaroche 1809, Risso 1810, Costa 1829, Canestrini 1872). Moreau (1881) was the first author to note that *A. tobianus* does not occur in the Mediterranean but others continued to recognize *A. tobianus* (Carus 1893, Lo Bianco 1909, Sanchez-Comendador 1904, Borja 1920, de Buen 1935, Bini 1968, Söljan, 1948, Reay 1986). Sabatés et al. (1990) felt that all references to sand eels in the Mediterranean prior to Duncker and Möhr's (1935, 1939) description of *Gymnammodytes* pertained to *G. cicereus*. These include all references to *A. tobianus*, *Ammodytes cicereus* (Rafinesque 1810), *Ammodytes argenteus* (Risso 1826), *Ammodytes siculus* (Swainson 1820-21, Günther 1862, Steindachner 1868) and *Ammodytes terebrans* (Cisternas 1875). Some limited *G. cicereus* to the Mediterranean and

G. semisquamatus to the northeast Atlantic (Gilbert 1912, Corbin 1950, Bas 1964, Wheeler 1969 and Tortonese 1975, 1987) while others believed *G. cicereus* was located both in the Mediterranean and Atlantic (Bini 1968, Wheeler 1973). However, Sabatés et al. (1990) extended range of *Gymnamodytes semisquamatus* into the Mediterranean and confirmed its sympatry with the endemic Mediterranean *G. cicereus*.

Herklotsina, Ammodytoides, Bleekeria and Embolichthys

Bleekeria was originally designated by Günther (1862) when he described *Bleekeria kallelepis*. He distinguished *Bleekeria* from *Ammodytes* mainly by absence of ventrolateral skin folds. *Bleekeria kallelepis* has the anterior section of its dorsal fin in a shallow groove, six branchiostegals and vent midway between root of caudal and the origin of pectoral. Four other nominal species of *Bleekeria* have been recognized (Ida, 1973), *B. vaga* McCulloch and Waite, *B. gilli* Bean, *B. renniei* Smith and *B. viridianguilla* Fowler. Bean's (1895) description of *B. gilli* contained a few subtle features separating it from *B. kallelepis*. He noted seven branchiostegals, entire length of dorsal and anal fins in a deep groove and vent closer to root of caudal than to origin of pectoral. McCulloch and Waite's (1916) work indicated *B. vaga* is closely allied to *B. gilli* except that its body is covered with rudimentary scales enveloped in oblique skin

folds and the row of scales beneath the dorsal fin has vertical tubules toward their posterior ends. These tubules disappear on more anterior scales.

Description of oblique skin folds on *B. vaga* is reminiscent of plicae on *Ammodytes* or *Hyperoplus* and is significant because they were not observed on other species of *Bleekeria* (Bean 1895, Günther 1862, Fowler 1931, Smith 1957) nor have I observed oblique folds on *Bleekeria renniei*, *B. gilli* or *B. viridianguilla*. No mention of oblique skin folds are found in other investigation of *Bleekeria vaga* either (Duncker and Möhr 1939, Ida 1973, Ida and Randall 1993). Perhaps McCulloch and Waite's (1916) description of *B. vaga* is inaccurate and they mistook oblique rows for folds? If that was the case then possibly these folds are similar to oblique rows described by Smith (1957) on *B. renniei* but Smith's (1957, fig.2, p. 220) drawings do not illustrate oblique rows, therefore it's hard to judge what he meant or the accuracy of McCulloch and Waite's (1916) description. Examination of the types may resolve this dilemma.

Fowler (1931) originally described *Herklotsina viridianguilla* but *Bleekeria viridianguilla* has been used extensively as a synonym (Duncker and Möhr 1939, Eschmeyer 1990, Stevens *et al.* 1984) although it is not clear whether *Herklotsina* is indeed synonymous with *Bleekeria* (Collette, pers. comm.). *Herklotsina* was distinguished from *Bleekeria*

by minute teeth in the jaws, larger eyes, a less forked caudal fin, different head physiognomy and brown cinnamon color. Apparently, Fowler (1931, fig. 13, p. 312) did not have an example of *Bleekeria* in front of him when he compared *Herklotsina* to *Bleekeria*. Instead he used the literature and the illustration of Day for *Bleekeria gilli* (1878, fig. 3, pl. 91, p. 420). *Bleekeria viridianguilla* apparently is more closely related to *Embolichthys mitsukurii* than other species of *Bleekeria* (Fig. 139) which effectively removes it from *Bleekeria*. Consequently, the results of this study raise more questions than answers concerning the systematic of *Herklotsina*. Should it be recognized as a distinct monotypic genus, combined with *Bleekeria* or placed in *Embolichthys*?

Beebe and Tee-Van (1938) described a new species *Ammodytes lucasanus*, acquired from stomachs of several species of fishes and one cormorant. It lacks the typical features of *Ammodytes* including scales in oblique rows and ventrolateral skin-folds and in that respect is more similar to *Bleekeria* or *Embolichthys*. Duncker and Möhr (1939) placed *A. lucasanus* in the synonymy of *B. gilli* and Collette (pers. comm.) concurred with this. Collette procured fresh ammodytid material collected on the Pacific Panamanian coast and the Galapagos and compared them to the types of *B. gilli* and *A. lucasanus*. His comparisons of number of anal fin rays, dorsal fin rays, pectoral fin rays, gill rakers on

first arch, vertebrae and total number of lateral line scales, indicates that all these specimens represent *Bleekeria gilli* Bean.

Systematics of *Bleekeria* is somewhat controversial because there are good reasons for placing *B. gilli*, *B. vaga* and *B. renniei* in the genus *Ammodytoides* (Duncker and Möhr 1939) because they share a complex set of ossicles and ligaments in the oral region (Ida 1973, Collette pers. comm., Ida pers. comm., Ida and Randall 1993). Ida discovered that extra ossicles in the oral region of *B. vaga*, *B. gilli* and *B. renniei* replace homologous cartilaginous tissues found in other ammodytids but he retained use of *Bleekeria* as the generic name for these species. However, in a recent paper by Ida and Randall (1993) describing a new Hawaiian species, *Ammodytoides kimurai*, they recognized the type species *Ammodytoides vagus* McCulloch and Waite (1916) and the species *Ammodytoides gilli* Bean (1895) and *Ammodytoides renniei* Smith (1957).

Bleekeria is in need of major revision and a careful reexamination of the type species *Bleekeria kallolepis* is pivotal. The scarcity of *Bleekeria* in museum collections has hindered this study but may also reflect a relative rarity in nature. One report described difficulty in catching *Ammodytoides* (Ida and Randall, 1993) which perhaps compounds this scarcity. Elucidation of relationships and taxonomy of the *Bleekeria* - *Ammodytoides* complex would also

be biogeographically interesting because their range spans the tropical Indo-Pacific region (Smith 1957, fig. 1, p. 219, Ida and Randall 1993).

Embolichthys contains two species, *Embolichthys mitsukurii* Jordan and Evermann (1903) and *Embolichthys sarisa* Robins and Böhlke (1970). *Embolichthys* was erected by Jordan (1903) for *Bleekeria mitsukurii* Jordan and Evermann (1902) because it has minute thoracic pelvics and no species of *Bleekeria* possesses pelvic fins. Other notable features in Jordan and Evermann's (1902) original description which suggested exclusion from *Bleekeria* included: smaller and firmer scales, dorsal fin in a groove and weak teeth on front of jaws. *Embolichthys sarisa* was taken at a depth of 187 meters over rocky bottom, off the island of St. Vincent in the Caribbean (Robins and Böhlke 1970). This was a notable discovery since other species of ammodytids are generally found in shallow seas over sandy substrates and it is the only record of an ammodytid in the tropical Atlantic. Compared to *Embolichthys mitsukurii*, *E. sarisa* has lesser body depth, scale less regularly arranged, scale margins more rounded and no teeth on the premaxilla or dentary, more dorsal and anal rays and less pored lateral line scales. Robins and Böhlke (1970) also commented on the shared occurrence of two closely spaced rays on the last dorsal pterygiophore of *Embolichthys sarisa*, *E. mitsukurii* and *Bleekeria viridanguilla* but made no mention of the

interrelationship of these species to each other or to the rest of the family.

Summary

Except for general comments on relationships of Atlantic and Pacific *Ammodytes* implied with statements about circumpolarity of *Ammodytes hexapturs* (Andriyashev 1954, Walters 1955, McAllister 1960 and Richards *et al.* 1963), proposal of a trans-Atlantic *Ammodytes americanus* - *Ammodytes marinus* complex (Winters and Dalley 1988) and division of ammodytids into two groups based on absence or presence of fanged vomers (Richards *et al.* 1963), no phylogenies of Ammodytidae have been formally presented. Duncker and Möhr (1939) revised the family but they dealt with nomenclature, synonymy and new species descriptions. Ida (per. comm.) outlined a systematic revision and rough phylogeny where the most primitive members of the family have well developed pelvics, lower number of vertebrae, less anal and dorsal fin ray counts and a lower ratio of abdominal to caudal vertebrae. Ida said that he intended to erect a new genus into which he would place the most plesiomorphic ammodytid, *Embolichthys sarisa*. This genus would be defined primarily by well developed pelvics. He believed that the biggest problem with Ammodytidae systematics is the genus *Ammodytes*, but as yet he has not

published his findings.

Review of the systematic history of Ammodytidae shows that, despite absence of phylogenetic hypotheses for species intrarelationships, the literature contains an unexploited character data base relevant to phylogenetic analysis. These characters include: ventrolateral skin folds, labial cartilages, ligaments and ossicles; post-larval pigmentation patterns; post-larval vomer morphology; lateral line and lateral line scale morphology; extent and depth of dorsal fin groove and patterns of scales on the body. Such characters were untested in a formal phylogenetic context but their informative potential is utilized in the following phylogenetic reconstruction of ammodytid relationships.

Materials and Methods

Clearing and staining followed procedures originally devised by Taylor (1967), refined with differential alcian blue stain for cartilage (Dinkerghus and Uhler 1977) and further revised by Taylor and VanDyke (1985), who discussed the importance of anhydrous alcian blue and buffered formalin fixation. I initially emulated procedures of Dinkerghus and Uhler (1977) but found some fish completely disarticulated after trypsin digestion and immersion in alizarin stain solution made with 1% KOH. This was probably due to inadequate or improper fixation of specimens, over digestion with trypsin (Taylor and Van Dyke 1985) and the causticity of 1% KOH.

Taylor and Van Dyke (1985) found that higher acidity of unbuffered formalin contributed to bone loss and degradation of connective tissue ultimately resulting in poor stain uptake by cartilage and skeletal disarticulation during trypsin digestion. Disarticulation was eliminated and cartilage stained vividly if freshly caught specimen were fixed in buffered 10% formalin prior to clearing and staining. They also found glacial acetic acid, in the alcian blue stain, hydrolyzes cartilage and connective tissue even if small quantities of water are present in specimen or stain solution. A specimen dehydrated in absolute alcohol and an alcian blue stain made with absolute alcohol practically eliminates this hydrolytic activity. Water also

dissolves stainable mucopolysaccharides in cartilage which decreases alcian blue binding. Consequently, anhydrous conditions optimize alcian blue staining (Taylor and Van Dyke 1985). Taylor and Van Dyke (1985) also discovered that specimens stored for extended periods in alcohol and not initially fixed in buffered formalin, did not stain well with alcian blue when refixed in buffered formalin, even under anhydrous conditions. Nonetheless, increased alcian blue binding was observed, on specimens whose original method of fixation could not be ascertained, by using buffered formalin fixation before staining and anhydrous staining procedures.

Improvement in quality of clearing and staining, with no disarticulation, resulted if procedures of Taylor and Van Dyke (1985) were complied with. Particular attention was given to these aspects of their procedure: fix specimens in calcium carbonate saturated 10% formalin for 2 to 3 days, avoid total water immersions after formalin fixation, gradually dehydrate specimens into absolute alcohol and stain for cartilage with anhydrous alcian blue, remove from first trypsin digestion before specimens are completely cleared with approximately 25% of muscle opaque and use 0.5% KOH in all alizarin staining and destaining steps.

After alizarin staining and the second digestion specimens were normally immersed for 24 hours each in successive glycerin - KOH solutions of 25%, 50%, 75%

glycerin - 0.5% KOH. However, in cases where sections of muscle tissue remained stubbornly opaque, I added hydrogen peroxide in ratio of ten drops per 100 ml of the 25% glycerin - 75% KOH [.5%] solution. Specimens and solution [specimen to solution volume, 1 to 10] were placed in clear glass jars laid horizontally on a white enamel tray under fluorescent light or direct sunlight. Light facilitates hydrogen peroxide bleaching and complete clearing usually followed in 2 to 4 days. Longer immersions of up to a week were sometimes necessary and had no adverse effects on the specimens. After this treatment transfers through the successively more concentrated glycerin - KOH solutions were continued. Cleared and stained fish are stored in 70% glycerine-30% distilled water solution instead of 100% glycerine normally recommended (Taylor 1965, Dingerkus and Uhler 1977, Taylor and VanDyke 1985). The lower viscosity and diffractive index of the 70% glycerin solution made work under the dissecting microscope much easier, eliminating streaking patterns caused when instruments disrupt the normally viscous 100% glycerine. A few thymol crystals were added to all final preparations as a preservative (Dingerkus and Uhler 1977, Taylor and VanDyke 1985).

Specimens were usually scaled prior to clearing and staining but scales, scale patterns and lateral line scales could easily be examined if skin and scales were left intact. Brightly colored scales resulted and made excellent

subjects for light microscopic examination. Undisturbed scales imbedded in cleared skin is also an instructive technique for observing scales patterns on body which sometimes were not easily observed on alcohol preserved material due to obscuring mucous, tissue debris and membranes. Skin and scales could just as easily be removed after clearing and staining to view the underlying skeleton if necessary.

Evisceration before clearing was not necessary on these small fishes either. With the body cavity filled, no appreciable hinderance of enzymatic trypsin digestion of deeper internal muscle tissues were observed, plus the gut and internal organs cleared and stained beautifully with alcian blue. Hence, gut morphology and its contents could be examined *in situ* which was an additional incentive not to eviscerate, besides the obvious benefit of saving time. If necessary, evisceration could always be done after clearing and staining is complete with internal organs retained for further study.

Scanning Electron and Light Microscopy

Scanning electron microscopy (SEM) was used to investigate bones, scales and skins from cleared and stained preparations and 75% ethanol preserved specimens. On selected cleared and stained specimens the following

preparative procedures were initiated. Fish were rinsed in 30% borate buffer and small patches of skin are removed from right side, midway between caudal fin and head. Parallel transverse incisions were made approximately 1.0 cm apart, from base of dorsal fin to mid-ventral surface. Cuts were connected by longitudinal incisions. The top incision was parallel to and just below dorsal fin and the bottom cut was made mid-ventrally. These rectangular pieces of skin included an abundant number of scales and a section of the lateral line. Skins were gradually dehydrated through increasing concentrations of alcohol-water solutions [15%, 45%, 75%, 95%, absolute alcohol] in small screw cap scintillation vials, containing approximately 50 mls. of solutions. One hour immersions in each concentration of ethanol was sufficient. Absolute alcohol was changed twice and the second immersion continued for at least 12 hours. At this point some scales were removed and mounted on microscope slides. Scales were carefully blotted between a folded piece of Whatman qualitative filter paper to remove excess alcohol. They were placed on 75 mm X 25 mm microscope slides and imbedded in Permunt, an acrylic resin (trademark name of Fisher Scientific Company), under a 22mm X 22mm cover slip.

Following alcohol dehydration, skins were transferred to anhydrous iso-amyl acetate, where they remained until critically point dried. Critical point drying completely

dehydrates a preparation without formation of destructive surface tension which can occur when water normally evaporates at ambient pressure (Coleman 1977). Critical point drying was performed in a Balzers CPD 030 instrument, using liquid carbon dioxide as the transition fluid. After drying, approximately five millimeter square patches of skin were cut and mounted on 12mm diameter aluminum SEM stubs by tacking down their corners with low resistance contact cement (E.F. Fullam 14820). Individual scales were removed from these skins with fine forceps and placed on double stick tape mounted next to skin patches on the stubs. The double stick tape is 3M brand obtained from E.F. Fullum (product number 17850). Grounding of tape to the stub ground was accomplished by applying a small drop of low resistance contact cement to each corner which acts as a conductive junction between tape and stub. Clearing and staining removed mucus and extraneous adhering tissue so while these preparations were fragile, their scales were clean and produced excellent SEM micrographs.

Skins from 75% ethanol preserved specimens were dissected and processed in a similar manner except their dehydration is started by immersions in 95% ethanol - water. However, their scales were frequently covered with mucous and debris, making them less useful for scanning electron micrographs, although whole skins produced good micrographs of lateral lines, plicae and ventro-lateral skin folds

(Figs. 69, 107).

Hughes (1981) went into great detail on methods of preparation of individual scales for scanning electron microscopy and the work remains a useful reference in this field. Her technique of cleaning scale surfaces in dilute bleach solution with a small artist brush was utilized and successfully removed troublesome mucus and membranes, especially on posterior fields of the tiniest, most delicate ammodytid scales. Excellent clean scale mounts were prepared in this manner. In addition, Hughes' suggestion of mounting scales while still pliable from alcohol minimized bothersome curling and cracking, which occurred if all solvent was evaporated prior to mounting.

Scales were removed primarily from specimens stored in 75% ethanol. They were detached from right side, midbody, approximately halfway between lateral line and ventral surface. Scales from other areas of the body and the lateral line were also sampled and are noted accordingly. Most scales retained membrane and debris on their lateral surfaces which required cleaning with sodium hypochlorite. They were placed in a watch glass filled with 1.5% Sodium Hypochlorite solution (common household bleach diluted 1 to 3.5 with distilled water). The surface was cleaned with an ultrafine 00 Windsor & Newton series 994 artist brush under a dissecting microscope. Careful monitoring of the scale was done because decalcification and disintegration can

occur quickly in bleach solution, especially if particularly fragile scales are immersed too long. Therefore, only one scale was prepared at a time.

Following sodium hypochlorite treatment, scales were placed in successively more concentrated ethanol-water solutions of 15%, 45%, 75%, 95% and absolute ethanol. A four sectioned watch glass contained the first four concentrations and scales were immersed in each solution for approximately 5 minutes. Final immersion for 15 minutes in absolute ethanol was done in a separate petri dish. Upon removal from absolute alcohol, the scale was blotted on Whatman qualitative filter paper to remove excess alcohol and transferred to 8mm squares of 3M brand double stick tape mounted on 12mm diameter SEM stubs. Tape was grounded in four corners with low resistance contact cement as previously described. Stubs were placed in a Bel-Art 149mm plastic vacuum desiccator containing Drierite indicating desiccant under a vacuum of approximately 127 Torr (1 Torr = standard physical atmospheric pressure/760). Prepared scales were stored in vacuum desiccator at ambient temperature for at least 12 hours before coating. Vacuum combined with desiccant draws out most water and alcohol in the scale and high vacuum of the coater results in virtually total dehydration.

The pelvic girdle of *Embolichthys mitsukurii* was dissected from an alcohol preserved specimen and most of

clinging muscle and tissue is removed in 75% ethanol under dissecting microscope. Final cleaning by immersion in 1.5% sodium hypochlorite solution was accomplished under the scope using fine forceps and artist brush. Individual pelvic bones are extremely delicate and separate quickly in bleach solution. Care must be taken because such small bones, like scales, can quickly disintegrate in bleach, but, osteological detail was preserved on separated bones by cautiously observing progress of tissue dissolution through the microscope. Despite its shortcomings, only bleach can effectively remove muscle and tissue on such small bones. Following defleshing, pelvics were dehydrated and mounted on stubs as previously described for scales from 75% alcohol preserved material.

A dry specimen is a very good insulator so a fine layer of conductive material, usually gold, is sputter coated on the surface in order to ground specimen. A Polaron Equipment Ltd. 5150 SEM coating unit is utilized to sputter coat 100 Angstrom layer of gold on to surface of stub, tape and prepared scales or bones. Proper grounding of specimen to tape and stub is essential for production of an accurate image. Unless there is a low resistance path to ground, electrons accumulate just below surface causing a degradation of the SEM image. The most common type of degradation is charging and it manifests as an extremely bright luminescence obscuring sections of the image. This

is caused by higher energy electrons emerging from a surface which is at lower potential than surrounding coated surfaces, due primarily to presence of water molecules in tissue (Pawley *et al.* 1975). If charging was a problem, final immersion in absolute alcohol is modified to include two changes of absolute alcohol lasting at least 12 hours each and storage of stub mounts in a vacuum oven at 60° C for at least 12 hours before coating. Coated mounts were routinely stored at ambient temperature in a vacuum desiccator, containing Drierite, at a pressure of 127 Torr in order to keep them dry.

Two models of scanning electron microscopes were employed in this study. A Zeiss 950, with a tungsten filament as the electron source, was used at the American Museum of Natural History and a Zeiss 940, with a lanthanum hexaboride LaB6 filament, was employed at the City College of New York. Most scanning electron micrographs were shot on Kodak 4X5 Technical Pan film, no. 4415 and a few were taken with Polaroid type 55, positive-negative 4X5 film. Contact prints were made in the photography department at the American Museum of Natural History.

Some scales were prepared for examination under light or dissecting microscopes. They were obtained from 75% ethanol preserved specimens and removed from middle of right side, under lateral line at approximately the center of body. Scales were cleaned in 1.5% sodium hypochlorite as described

above and immediately placed in .5% KOH - Alizarin Red S solution made per instructions of Taylor and VanDyke (1985). Acidity of bleach solution is quickly neutralized in KOH and scales could remain in stain overnight without adverse effects. Overnight staining is followed by five minute successive immersions in approximately 5 ml. ethanol-water solutions made with following percentages of ethanol, 15%, 45%, 75%, 95% and absolute alcohol. After alcohol dehydration one to three scales, depending on their size, were placed on a 75mm X 25mm glass slide with a drop of absolute alcohol. Twenty two millimeter square coverslips were placed on top of scales to keep them flat as alcohol evaporated. The alcohol drop evaporated quickly but preparations were left overnight so as much of the solvent as possible is removed. In majority of cases, especially for small or fragile scales, weight of coverslip is enough to keep scales flat but some additional weight was necessary for larger scales. In such cases, a scintillation vial filled with sand and placed on top of coverslip was usually sufficient mass. Following overnight drying, the coverslip is removed, a generous drop of Permunt is placed on the scales and new coverslip applied. Excellent results were obtained with this simple procedure, producing brightly red stained flat scales, permanently mounted on microscope slides.

Light microscopic observations and photographs were

made with Wild model M20-70051 microscope fitted with V 1.25X photo extension tube or Wild model M7a dissecting microscope with Wild TYP 352873 photo extension tube. Mounted on either photo tube is a Wild 2209 lens and shutter apparatus used in conjunction with Wild Mka4 automatic camera controlled by Wild MEL 13 Photoautomat. A 6X photo eyepiece is placed in barrel of photo extension tube on the dissecting scope and a 10X eyepiece is used on the microscope. Shutter of the automatic camera is kept open permanently by a control on Photoautomat and a Pentax K1000 camera body was bayoneted on lens-shutter housing with combination of T-mounts and extension spacers. Parfocality was checked by placing cross hair reticle on the stage, focusing on it through magnifying eyepiece placed over square of ground glass covering film plane of the 35 mm camera body and then focusing on cross hairs through open eyepiece of microscope. Parfocality is achieved when the image is exactly focused at camera film plane or eyepiece. Gross adjustments were made by adding or subtracting large diameter O-rings between the extension spacers. Fine focusing was done through an adjustable open eyepiece (Wild 10X/21). Subsequent focusing could be done through range finder of camera but eyepiece of microscope is better because it gives a much sharper image. Ekatchrome 50T and 64T tungsten slide film or Ektachrome 64 daylight negative film, used in conjunction with 80A Wratten filter for color

balance, were used to record images. The light meter in the Pentax was employed for exposure settings and aperture was usually opened one stop greater than meter indicated. Prints made from slides were generally sharper and had better color balance (Fig. 96) than negative print film. Drawings are made with assistance of a Wild TYP 256575 drawing tube adapter on model M7a scope.

Phylogenetic Analytical Techniques

Relationships of Ammodytidae were determined by principles of phylogenetic systematics formulated Hennig (1950). A 1966 translation (Hennig 1966) of Hennig's book strongly influenced contemporary systematic methodology and remains the most widely accepted paradigm in current systematic theory. For Hennig, only shared derived characters, termed synapomorphies, are evidence of relationship. Groups of organisms sharing synapomorphies are called monophyletic and a classification of organisms is based upon a hierarchy of synapomorphies. Primitive characters are not useful, except at the level in the hierarchy where they first appeared since at that level they are synapomorphies. Shared primitive characters or symplesiomorphies, erroneously place organisms into groups not defined by common ancestry and lead to grouping schemes termed paraphyletic (Hennig 1966).

A vast literature, including entire journals such as *Cladistics* and *Systematic Zoology*, are now devoted to discussion of relationships and methodologies based upon general rules that Hennig discussed in his treatise. Use of branching diagrams to describe hierarchical ordering of synapomorphies and phylogenetic relationships are ubiquitous in this literature. A new scientific specialization arose, termed cladistics, which deals with rules and methodologies governing formulation of synapomophy schemes and branching diagrams. Much of the literature is fueled by debates on application of cladistic principles and new methodologies. Discussions concerning principles of phylogenetic systematics and cladistics can be found in Wiley (1981), Nelson and Platnick (1981), Janvier (1984) and Schoch, (1986). Application of cladistics in biogeography are common but Brundin (1966) and Rosen (1975) are frequently cited pioneering works.

Modern computer technology has revolutionized cladistics and systematics by making phylogenetics accessible to virtually anyone with knowledge of a particular group of organisms. Data matrices with both large and small numbers of taxa can be analyzed by programs which output all most parsimonious trees depicting relationships of these taxa (Farris 1988, Swofford 1991a). Facility of this computer software has made their application pervasive in systematics and it is now possible

to manipulate and code increasingly larger data sets derived from nucleotide sequence data (Morden and Golden 1989) or combined molecular and morphological data (Wheeler *et al.* 1993).

The following programs were used to evaluate relationships of Ammodytidae: PAUP version 3.1 (Swofford 1993), Hennig86 version 1.5 (Farris 1988) and TAX 3.0 (Nelson and Ladiges 1992). PAUP and Hennig 86 are cladistic parsimony programs which use different tree searching algorithms (Swofford 1993) but generate virtually identical results, except when there are missing entries due to unknown data, inapplicable characters or polymorphic taxa (Platnick *et al.* 1991). PAUP is more user friendly but Hennig86 with its cryptic commands and parsimonious syntax is actually faster and more streamline. PAUP is useful because the input matrix is limited only by the size of the computer's memory. This last capability can be employed when large three taxon transformation matrices generated by TAX, are analyzed. TAX (Nelson and Ladiges 1992) converts original character data into all possible combinations of 3 taxon statements that are contained in the original characters. Characters transformed in this way are reduced to the most basic informative taxonomic unit, three taxa. Data generated by TAX is coded as a text file in PAUP file format and then translated to MacIntosh text file format by Apple File Exchange Program Ver 1.1.3, Apple Computer Inc.

MacIntosh text files can be routinely read into PAUP if they have either the PAUP or Hennig86 file format.

This study has abundant missing data because of deficiencies in observations for species of *Bleekeria* and *Embolichthys sarisa* due to difficulty in obtaining permission to clear, stain and dissect rare specimens. When character matrices contain missing data, computer programs generate spurious results not supported by data (Platnick et al. 1991, Nelson and Ladiges 1993). This situation has never been adequately addressed by PAUP or Hennig86. On the other hand, three-item analysis (Nelson and Ladiges 1993) generates transformations matrices full of missing entries, due to the transformation algorithm and computes many trees with spurious nodes. However, the strict consensus tree of all three-taxon transformation trees is the correct tree if original data is 100% consistent (Nelson and Ladiges 1993). Consequently, three taxon analysis might minimize effects of spurious nodes due to missing data in original matrix at any consistency index and this effect might be more pronounced as consistency indices increase, but no empirical evidence has proven this true. Experiments designed to show this phenomena have not been done such as observing relationships between consistency indices of trees generated by conventional parsimony on data sets with missing enteries and those from 3-taxon analysis on same data sets with original data set optimized on. Hence, three item analysis

is untested as a method for resolving problems associated with missing data. Platnick *et al.* (1991) suggested that future cladistic parsimony software suppress spurious components or the systematist '...should check the character optimization at each node carefully, to ensure that no nodes are supported only by mutually exclusive optimizations of the same character(s).' (Platnick *et al.* 1991, p. 341). In any case, use of three item analysis is experimental, but because treatment of characters in this way emphasizes differences in information content of each character and may be more susceptible to influences from patterns of relationships hidden in scattered data (Nelson and Platnick 1991), its implementation could reveal new perspectives on relationship.

Polarizing character states follows rules proposed by Maddison *et al.* (1984, p. 83). They suggested using a simultaneous parsimony analysis on both ingroup and outgroup. This eliminates any cases where less than most globally parsimonious trees are found due to misapplication of Watrous and Wheeler's (1981) rule when outgroup relationships are poorly known.

Ordering of some multistate characters were done in accordance with suggestions of Lipscomb (1992) who determined transformation series by a two step process. These steps are: (1) order states so that those most similar to each other are adjacent and (2) test the hypothesis of

transformations by observing amount of congruence between groups defined by transformations and groupings generated by other character data. This method stressed homology of adjacent states and satisfies criteria of parsimony such that 'the fewest assumptions of both character state change and appearance and persistence of states.' (Lipscomb 1992, p. 50) are made. Lipscomb (1992) argued that non-additive character analysis and transformation series analysis (TSA) are not necessarily the most parsimonious procedures since they can generate hypotheses that have a greater number of assumptions concerning multistate character appearances, persistence or change.

Phylogenetic hypotheses formed the basis for definitions of various teleostean subgroups. Hypotheses of acanthomorph relationships and definition of subgroups were derived from the work of Greenwood *et al.* (1993), Lauder and Leim (1983), Rosen (1973, 1985), Stiassny (1986, 1993), Johnson (1992) and Johnson and Patterson (1993). Percomorpha were recently redefined by Johnson and Patterson (1993) but Perciformes remain problematic such that they cannot be described by a single synapomorphy (Lauder and Leim 1983, Johnson and Patterson 1993). Recent efforts have removed synbranchiform and gasterosteiforms (Johnson and Patterson 1993) and Mugiloidei (Stiassny 1993) but most groups included in Perciformes basically follow tradition (Nelson 1984). Thus Perciformes are Percomorpha minus

Synbranchiiformes, *Elassoma*, Gasterosteiformes, Mugiloidei and Atherinomorpha (Johnson and Patterson 1993). Definition of trachinoid fishes is based on work of Pietsch (1989) who found ten traditional trachinoid families related cladistically but some aspects of this assemblage are difficult to accept (Johnson 1993, Mooi and Johnson 1993). Percoids follow a list compiled by Johnson (1984).

Scale Character Nomenclature

Scales of representative species, from a list of percoid families with cycloid scales (Johnson 1984), trachinoids (Pietsch and Zebatian 1990) and indicator species used by Johnson and Patterson (1993), were examined. A broad survey of acanthomorph scales was necessary for determination of apomorphic and plesiomorphic lepidologies because the polarity of characters derived from scale fields has never been done.

The nomenclature of Lagler (1947) and McCully (1961) is followed in describing scale morphology. Unique structure were discovered on ammodytid scales which required definition of some new terms. These definitions will be given in the *Character Survey* section as their scales are described. *Ridges* or *Circuli* (Fig. 29, **CONR**) are raised concentrically oriented structures generally following the outline of the scale. *Scalelets* (Fig. 12, **AFS**) were defined

by McCully (1961) as structures on bony plate of the scale separated from each other by gaps or grooves called *sulci*. Radial sulci originating at the nucleus and terminating on anterior margin (Fig. 12, **SUL**) are designated *primary sulci* and scalelets bordered by primary sulci are termed *primary scalelets* (Fig. 12, **AFS**). *Secondary scalelets* (Fig. 13, **SSC**) are sections of the scale plate defined by *secondary sulci* which are incomplete radial sulci. In other words, secondary sulci do not trace a path from nucleus to scale margin (McCully 1961). Articulated spines or cteni of the posterior field were also called scalelets by McCully but for sake of clarity, the definitions of Roberts (1993) for posterior field spines and cteni will be used. Thus, scalelets refer to section of the scale demarcated by sulci, either primary or secondary. McCully described *secondary ridges* as distinct spurs coming off the main concentric ridges or as unconnected segments in the nucleus (Figs. 96, 97, **LFSR**). The *Nucleus* (**NUC**) is the central portion of the scale and is generally bounded by the innermost concentric ridge (Fig. 29) but may be amorphous (Fig. 12). It is either smooth (Fig. 29) or contains secondary ridges (Fig. 12).

Euteleostean scales can be divided into three classes which roughly correlate with a linear transformation series of primitive to derived. These categories are cycloid, two field and four field scales. The plesiomorphic scale is

cycloid and the most derived scales have four fields. An intermediate type, I refer to as two field scales, generally occurs in groups that are considered more derived than taxa with cycloid scales but primitive relative to taxa which have four field scales.

Cycloid scales are defined by series of concentric ridges (Fig. 29, **CONR**) encircling entire scale, with no field definition, scalelets or other structural detail (Figs. 28, 29, 31, 33). Less derived teleosts such as *Parasudus* (Fig. 29) or salmonids (Järvi and Menzi 1936) possess this type of cycloid scales but the perciforms, *Rachycentridae* (Fig. 28), *Echeneididae* (Fig. 31) and *Coryphaenidae* (Fig. 27), also exhibit them. Some cycloid scales show folding on their anterior fields (Fig. 29, **FD**) but concentric ridges are not interrupted by these folds.

Two field scales have anterior field scalelets (Fig. 10, **AFS**) separated by sulci (Fig. 10, **SUL**). The remainder of the scale is adorned only by concentric ridges (Fig. 10, **CONR**). Such scales are found on many poeciliids (Lanzing and Higginbotham 1974) cyprinodonts (Fig. 54) and mugilids (Lui and Shen 1991). They seem particularly common in atherinomorph taxa but are also observed on some perciforms (Figs. 10, 47, 50, 53).

Scales of serranids (McCully 1961, Lagler 1947), percoids (Lagler 1947), mugilids (Lui and Shen 1991) and ammodytids (Fig. 12) show four fields. The fields are

approximately triangular with their vertices converging on the nucleus. Fields are defined relative to scale orientation on the fish. Thus, the *anterior* field (Fig. 12, **ANT**) is embedded in the skin and nearer to head and posterior field (Fig. 12, **POST**) is exposed and faces caudal fin. Two lateral fields (Fig. 12, **LAT**) occur dorsal or ventral to bisecting longitudinal axis of the scale. Each field of true four field scales has its own unique lepidology except the two lateral fields, which are in most cases mirror images of each other. Other terms have been mentioned for the fields such as dorsal and ventral for lateral fields and focus for nucleus (Lui and Shen 1991, Lagler 1947).

Selection of Outgroups and Preliminary Phylogenetic Analysis

Pietsch and Zebatian's (1990) alignment of ammodytids with trachinoids seemed tenable in some respects. The hypothesis for sister group relationship of ammodytids to uranoscopids-trachinids (Pietsch and Zebatian 1990) is one of the strongest nodes on the tree (Johnson 1993). However, lack of synapomorphies derived from key elements of their osteology such as gill arches, caudal skeleton, suspensorium and median fin supports precipitated skepticism as well (Johnson 1993).

In testing Pietsch and Zebatian's (1990) hypothesis, I

uncovered some wrongly coded character states and new characters which had bearing on selection of an outgroup. *Embolichthys mitsukurii*, their exemplar of Ammodytidae, actually lacks many characters used as synapomorphies for an Ammodytidae, Uranoscopidae and Trachinidae clade so I included all genera of ammodytids in their data matrix to more accurately represent the family.

The following revisions and additions are made to Pietsch and Zebatian's (1990) data set (Tab. 7). Character numbers are the same as those used by Pietsch and Zebatian (1990) and state after the character number is the modified change in state. Zero is plesiomorphic and one derived. *Embolichthys*, *Bleekeria* and *Gymnammodytes* do not have an epidermal covering united between adjacent scales (character 9, state 0) nor scales in oblique rows (character 20, state 0). Instead, *Embolichthys*, *Bleekeria* and *Gymnammodytes* have scales oriented parallel to horizontal axis of body (character 21, state 0). Examination of gill arches of *Embolichthys mitsukurii* revealed that it does indeed have tiny toothplates on the hypobranchials (Fig. 118, **HTP**), (character 15, state 0). Large well ossified extrascapulars comparable in size to those of *Embolichthys mitsukurii* (Pietsch and Zebatian 1990, fig. 2) are found on *Trichonotops* sp. (Fig. 119, **ES**), (character 17, state 1). Their medial extrascapular is fused to the parietal and contacts the anterolateral edge of the supraoccipital (Fig.

119) unlike the posteromedial margin contact of the supraoccipital described by Pietsch (1989, figs. 8, 15) for trachinids and some uranoscopids. The greatly restricted anterodorsal section of the hyohyoidei adductores muscle found in *E. mitsukurii* (Fig. 121, **HYO-AD**) also occurs in *Trichonotops multistriatus*, and *Trichonotops* sp. 1 and 2 (Fig. 122) so character (18) is recoded to accommodate this new finding (state 1). The description of the posterolateral expansion of the epiotics (character 23, state 1) is changed to more accurately reflect a small triangular shelf shared by ammodytids (Fig. 119, **EPOS**), uranoscopids (Pietsch 1989, figs. 10 & 11, Pietsch and Zebatian 1990, figs. 2 & 3) and trichonotids (Fig. 120, **EPOS**). Coding of Pietsch and Zebatian's (1990) scale character (4) is revised with a multistate unordered character representing the actual diversity these scales exhibit instead of a cycloid (state 0) or ctenoid (state 1) two state character. Coding is as follows: (0) transformed ctenoid, (Figs. 25, 56); (1) trachinid type, (Fig. 11); (2) uranoscopid, (Fig. 9); (3) ammodytid type, (Figs. 11, 12); (4) leptoscopid, (Fig. 24). Characters 30 and 31 are deleted because they forced monophyly of trichonotids, creediids and percophids but are not based upon any apparent synapomorphies. Inclusion of Champsodontidae with trachinoids (Pietsch 1989, Pietsch and Zebatian 1990) was convincingly refuted by Mooi and Johnson (1993). Therefore,

Champsodontidae are removed from further consideration.

Twelve characters are added to the data set which are synapomorphies for Ammodytidae and generic subgroups. Characters are listed in order and correspond to characters 32-43 of Table 7. Absence of character is considered primitive unless otherwise noted.

- (1) Large oval foramen in dentary (Fig. 110, **FOR**).
- (2) Multistate character describing the terminal lateral line scale. State (1) represents an enclosed canal on the terminal lateral line scale (Figs. 18, 19) and state (2) describes the scale with an open groove (Fig. 20).
- (3) Scales rounded and elongate in the dorso-ventral axis (Figs. 74-77, 80, 95, state 1). *Embolichthys* shows the primitive condition with a pentagonal shaped scale (Fig. 12).
- (4) An elongate anterodorsal process of suboperculum extending almost to posterior arm of hyomandibula (Figs. 113, 114, **SOPP**, state 1). Short process is plesiomorphic (Fig. 111, state 0).
- (5) Dorsally directed process on the interoperculars (Figs. 111-114, **IOPP**, state 1). Prominent crest and short anterior process is plesiomorphic (state 0).
- (6) A flattened supraoccipital with a greatly reduced crest, prominent anterior process and posterolateral wings of laminar bone (Fig. 115).

(7)

Symphysial process on dentary (Fig. 110, **SYMP**).

- (8) Metapterygoid process (Fig. 129, **MTP**).
- (9) Shelf on anterior margin of opercular, below hyomandibula (Figs. 112, 113, **OPS**).
- (10) Extra labial ossicles and cartilages (Fig. 110, **L2, L6, MD, MV, MPLP**).
- (11) Ventro-lateral skin folds (Fig. 4b, **VLSF**).
- (12) Radial ridges between scalelets in the anterior field (Figs. 73-79, **AFRR**).

Reanalysis of the revised data set (Tab. 7) did not challenge the sister group relationships of ammodytids and uranoscopids plus trachinids (Pietsch and Zebatiens 1990). However, these additions and modifications have a profound effect on tree topology (Figs. 2a, 2b) and collapsed much of Pietsch and Zebatian's resolution moving trichonotids into a polytomous relationship with ammodytids and trachinids - uranoscopids. Consequently, an outgroup comprised of trichonotids, uranoscopids and trachinids was chosen for this phylogenetic analysis of Ammodytidae (Fig. 2b).

Manipulation of Pietsch and Zebatian's (1990) data set by inclusion of modifications previously outlined produced a fully resolved cladogram of ammodytid generic relationships. Monophyly of Ammodytidae is supported by these synapomorphies: symphysial process on dentary, large foramen in dentary, metapterygoid process, shelf on anterior margin of operculum, extra-labial cartilages or ossicles. *Ammodytes*, *Bleekeria* (minus *B. viridianguilla*), *Hyperoplus*

and *Gymnammodytes* are united by sharing rounded or elliptical scales (Figs. 74-77, 80, 95). *Ammodytes*, *Hyperoplus* and *Gymnammodytes* are defined by ventrolateral skin folds and modified elongate terminal lateral line scale with perforated groove. Sister group relationship of *Ammodytes* and *Hyperoplus* is justified by shared specializations of scales in oblique rows and epidermal covering united between scales but these two characters are homoplasies also observed in trachinids and uranoscopids.

Taxonomic Units

Taxonomic units used in this study were based upon original descriptions, characterizations from the literature and geographic distribution. Ammodytidae biogeography is useful for characterizing some species because there are many endemic forms, especially in the northeast Atlantic.

The following species of *Ammodytes* are used in this study: *Ammodytes americanus* Dekay (1842), *Ammodytes dubius* Reinhardt (1838), *Ammodytes hexapterus* Pallus (1811), *Ammodytes tobianus* Linnaeus (1758), *Ammodytes marinus* Raitt (1934) and *Ammodytes personatus* Girard (1857). Tables 2 and 3 are synopses of meristic data on species of *Ammodytes*. Examination of the tables indicate that *Ammodytes* can be distinguished by a combination of meristics and biogeography.

Fishes designated as *Ammodytes americanus* and *Ammodytes hexapterus* have roughly the same meristic counts and have been postulated as part of a circumpolar complex (Andriyashev 1954, Walters 1955, McAllister 1960 and Richards et al. 1963) but no concrete evidence (ie. gene flow) has shown this to be true. Consequently, *Ammodytes hexapterus* is considered a distinct species with a Pacific range (Reay 1970, Kobayashi 1961, Hashimoto 1984, 1991, Okamoto 1981) and *A. americanus* occurs exclusively in the northwest Atlantic (Nizinski et al. (1990), Reay 1970, Leim and Scott 1966). *Ammodytes americanus* and *Ammodytes dubius* are effectively segregated by meristics in the northwest Atlantic (Nizinski et al. 1990).

Ammodytes marinus could either be aligned with *A. americanus* or *A. hexapterus*, but it has a slightly higher average number of counts and no demonstrable gene flow with other *Ammodytes* species implies it is distinct. In addition, endemism of northeast Atlantic *Hyperoplus* and *Ammodytes tobianus*, occurrence of *Gymnammodytes semisquamatus* only in northeast Atlantic and Mediterranean and western Greenland boundary of *Ammodytes dubius* (Einarrson 1951, Jensen 1944, 1941) suggests segregation of Atlantic *Ammodytes* into two isolated biogeographic assemblages (northeast Atlantic: *A. tobianus*, *A. marinus* and northwest Atlantic: *A. americanus*, *A. dubius*) is justified. Thus, it could be that the same mechanisms which caused

isolation of *Hyperoplus* and *Gymnamodytes* in the northeast Atlantic prompted the vicariance of northeast Atlantic *Ammodytes tobianus* and *A. marinus* from northwest Atlantic *A. americanus* and *A. dubius*.

Ammodytes personatus and *Ammodytes tobianus* have approximately the same number of vertebrae but as previously noted *A. tobianus* has distinguishing external morphological features and a northeast Atlantic distribution which clearly separates it from all other species of *Ammodytes* (Reay 1970). *Ammodytes personatus* is confined to the Pacific Ocean but it is found off Japan and the West Coast of North America. In Japan at least, it is latitudinally sympatric with *A. hexapterus* but distributed in different habitats (Okamoto et al. 1989, Hashimoto 1991).

The genus *Hyperoplus* (Günther 1862) is easily characterized by fanged vomers (Einarsson 1951, Reay 1986) and heavy post-larval pigmentation (Macer 1967, Corbin and Vati 1949). *Hyperoplus immaculatus* (Corbin 1950) can be separated from *Hyperoplus lanceolatus* (LeSauvage 1824) by the morphology of its vomerine teeth and higher dorsal fin ray and vertebral counts (Reay 1986). Low, almost separate cusps distinguish vomerine teeth of *H. immaculatus* and a single bicuspid tooth differentiates *H. lanceolatus* (Reay 1986, fig. 5, p. 945).

Gymnamodytes (Duncker and Möhr 1935, 1939) is characterized by scaleless anterior two thirds of its body

and scaleless lateral line composed of vertical and horizontal tubules. All three species in the genus *Gymnamodytes* were utilized in this analysis:

Gymnamodytes cicerelus (Rafinesque 1810), *Gymnamodytes semisquamatus* (Jourdain 1879) and *Gymnamodytes capensis* (Barnard 1927). They can easily be distinguished by extent of ventrolateral skinfolds or biogeographic distribution. Sabatés *et al.* (1990) clearly showed that *G. cicerulus* is endemic to Mediterranean and could be separated from the other two species by exhibiting ventro-lateral skin folds terminating past anterior end of anal fin. South African, *G. capensis* and northeast Atlantic *G. semisquamatus* have skin folds ending just past tip of the pectoral fin.

Three species of *Bleekeria* (Günther 1862) were examined for this study: *Bleekeria gilli* Bean (1895), *Bleekeria renniei* Smith (1957) and *Bleekeria viridianguilla* Fowler (1931). *Bleekeria gilli* is an eastern Pacific form, found from the west coast of Baja California to Ecuador (Bean 1895, Duncker and Möhr 1939, Smith 1957, Smith 1957, Collette MS). South African *Bleekeria renniei* (Smith 1957, fig. 2, p. 220) has anterior rays of anal fin forming a rounded lobe and highest number of dorsal and anal fin rays and vertebrae compared to other species of *Bleekeria*. *Bleekeria viridianguilla* is a western Pacific form (Fowler 1931) and can be distinguished from other species of *Bleekeria* by minute teeth in jaws, larger eyes, a less

forked caudal fin, different head physiognomy and hard robust scales.

Embolichthys (Jordan 1903) is primarily characterized by minute jugular pelvic fins and is the only ammodytid genus with pelvics. Both species were procured for this study and they can be easily separated by morphology of their scales. *Embolichthys mitsukurii* (Robins and Böhlke 1970) has well ossified, pentagonally shaped scales with four field converging at nucleus (Fig. 12). *Embolichthys sarisa* (Robins and Bohlke 1970) shows scales with a more rounded outline, numerous concentric ridges in posterior field and distinctive membranous cteni posterior to these circuli (Fig. 58).

Abbreviations Used in Tables and Figures

ACC	accessory cartilage
AF	anterior field
AFP	anal fin pterygiophore
AFR	anal fin ray
AFRR	anterior field radial ridge
AFS	anterior field scalelet
AFSR	anterior field scalelet ridge
ANT	anterior field
AR	articular
BB	basibranchials
BO	basioccipital
BOAP	anterior process of basioccipital
BOC	basioccipital crest
BOPL	basioccipital posterior laminar bone
BS	branchiostegal
C	ceratobranchials
CART	cartilage of fin articulation surface (pelvic bone)
CONR	concentric ridge
CP	central part (pelvic bone)
DEN	dentary
DFP	dorsal fin pterygiophore
DFR	dorsal fin ray
E	epibranchials

EC	ethmoid cartilage
ECT	ectopterygoid
END	endopterygoid
ENR	epinueral rib
EO	exoccipital
ES	extrascapular
ES-F	extrascapular fused to parietal
EP	epural
EPO	epiotic
EPOS	shelf of bone on epiotic
EPR	epiplueral rib
EVW	external ventral wing (pelvic bone)
FR	frontal
FOR	oval foramen in dentary
FPS	folded protoscalelet
GR	gill raker
H	hypobranchials
HP	hyomandibular process
HPU	haemal spine
HTP	hypobranchial tooth plate
HS	hyomandibular spur
HYO	hyomandibular
HYO-A	hyohyoideus adductores muscle
HYP	hypural
IAC	interarcual cartilage
INT	interopercular

IO	infraorbital
IOP	interopercular
IOPP	dorsally directed interopercular process
IW	internal wing (pelvic bone)
L1, L6	labial ossicles one, six
LAT	lateral field
LE	lateral ethmoid
LE-AE	lateral ethmoid anterior extension
LE-POP	lateral ethmoid postorbital process
LEP	lepidonts
LFSR	lateral field secondary ridge
LFCR	lateral field concentric ridge
LLC	lateral line canal
LLP	lateral line posterior pore
MD	maxillo-dentary ossicle
ME	mesethmoid
ME-LP	mesethmoid lateral process
MPLP-F	fused maxillo-premaxillary and lateral maxillo-premaxillary.
MTP	metapterygoid process
MTSP	secondary metapterygoid process
MXCC	maxillary cranial condyle
MXCP	maxillary cranial process
MXCP-MP	median process off base of maxillary cranial process
MXMP	maxillary medial process

MV	maxillo-vomerine ossicle
MES	mesopterygoid
MX	maxilla
NA	nasal
NAPZYG	prezygopophyseal neural arch
NS, NPU	neural spine
NU	nucleus or focus
OP	opercular
OPS	opercular shelf
PA	parietal
PAL	palatine
PB	pharyngobranchials
PFRR	posterior field radial ridges.
POST	posterior field
PHYP	parhypural
PMX	premaxilla
PMX-ART	articular process of premaxilla
PMX-ASC	ascending process of premaxilla
PMX-PM	postmaxillary process
POP	preopercular
PP	posterior process (pelvic bone)
PR	pleural rib
PTM	post temporal
PU	preural centrum
PU2vt	preural ventral radials
QU	quadrate

RV	radial valley
SN	supraneural
SOP	subopercular
SOPP	dorsally directed subopercular process
SPH	sphenotic
SUL	sulci
SYMP	symphyseal process
TP	tooth plate
U	ural centrum
UN	uronueral
UNC-PR	uncinate process
UP	upper pharyngeal teeth (-F or -U fused or unfused with endoskeleton)
V	vertebrae
VLSF	ventrolateral skin fold
VO	vomer
VO-LP	vomerine lateral process

Institutional Abbreviations

Institutional abbreviations follow the symbolic codes of Leviton et al. (1985).

- AMNH, American Museum of Natural History, New York
- AMS, Australian Museum, Sydney
- ANSP, Academy of Natural Sciences, Philadelphia
- BMNH, The Natural History Museum (British Museum), London
- BPBM, Bernice P. Bishop Museum, Honolulu
- CAS, California Academy of Sciences, San Francisco
- CAS-SU, California Academy of Sciences, San Francisco (from
Stanford University)
- CSIRO, Commonwealth Science & Industrial Research
Organization, Division of Fisheries & Oceanography, New
South Wales, Australia
- DAFS, Marine Laboratory, Department of Agriculture and
Fisheries for Scotland, Aberdeen Instituto de Ciencias
del Mar, Barcelona, ICM
- NHRM, Naturhistoriska Riksmuseet, Stockholm
- RINPF, Research Institute of North Pacific Fisheries,
Hokkaido University, Hakodate, Japan
- ROM, Royal Ontario Museum, Ontario
- RUSI, J.L.B. Smith Institute of Ichthyology, Rhodes
University, Grahamstown, South Africa
- UAM, University of Alaska Museum, Fairbanks, UAM

USNM, National Museum of Natural History, Washington, D.C.

UW, University of Washington, Seattle

ZMB, Museum für Naturkunde der Humboldt-Universität zu
Berlin, Zoologisches Museum, Berlin

ZMH, Zoologisches Institut und Zoologisches Museum, Hamburg

Specimens Examined

Number of specimens examined or used follow the catalog number or biogeographic information. Entries without a digit for number of specimens examined indicate only one individual was perused. All specimens examined were alcohol preserved except as noted otherwise. Those with C&S indicate cleared and stained material. Catalog numbers from the Ichthyology Department at the American Museum of Natural History with SD appended signify skeletons and those with SW designate cleared and stained specimens.

Elopidae

Elops saurus, AMNH 90860SD, Gulf of Mexico.

Megalopidae

Megalops atlanticus, AMNH 90706SD, Gulf of Mexico.

Albulidae

Albula vulpes, AMNH 56926SD, Magueyez Island, Vicinity of
La Parguera, Caribbean Sea, Puerto Rico.

Clupeidae

Alosa chrysochloris, AMNH 67630, Mississippi River, Lake
Providence, Louisiana, 5.

Congridae

Conger oceanicus, AMNH 56502SD, No data.

Gonorynchidae

Gonorhynchus greyi, AMNH 32972.

Esocidae

Esox niger, AMNH 62786.

Osmeridae

Osmerus mordax, AMNH 40726, Ithaca, Fall Creek, New York, 1
C&S.

O. mordax, AMNH 2220, Woods Hole.

Salmonidae

Salmo gairdneri, AMNH 63771, Anthony Creek, Tennessee, 6.

Sternotychidae

Sternoptyx diaphana, AMNH 29768SW, Kona Coast, Hawaii, 1
C&S.

Aulopididae

Aulopus purpurissatus, AMNH 92089SD, Port Phillip Bay and
Bass Strait (Melbourne Fish Market).

Aulopus japonicus, AMNH 13024, Misaki, Japan, 3, 1 C&S.

A. japonicus, AMNH 28636, Misaki Biological Station, Japan.

Gonorrhynchus greyi, AMNH 32972.

Chlorophthalmidae

Chlorophthalmus, AMNH 095767SD, Port Phillip Bay and Bass
Strait, (Melbourne Fish Market).

Chlorophthalmus agassizi, AMNH 27402, Venezuela, 1 C&S.

C. agassizi, AMNH 76024, Western Central Atlantic Ocean, 5.

Parasudis truculenta, AMNH 76017, South Carolina, 2.

P. truculenta, AMNH 53088, 36°30.6'N, 74°44.3'W.

Alepisauridae

Alepisaurus ferox, AMNH 69066SD, Virginia Beach, Virginia.

Synodontidae

Synodus foetens, AMNH 79670SD, Alabama, Gulf of Mexico.

Neoscopelidae

Neoscopelus macrolepidotus, AMNH 27405SW, Caribbean Sea,

16°35'N, 80°10'W, 1 C&S.

N. macrolepidotus, AMNH 73742.

Myctophidae

Myctophum obtusirostris, AMNH 25022, Fortune Island,

Bahamas, 2.

Percopsidae

Percopsis omiscomaycus, AMNH 41145SW, Hoosic River at Little

Hoosic, Rensselaer Co., New York, 1 C&S.

P. omiscomaycus, AMNH 42327, 2.

Aphredoderidae

Aphredoderus sayanus, AMNH 27432, Styx River, Alachua,

Florida, 5 C&S.

A. sayanus, AMNH 50907, Long Island, NY.

Gadidae

Gadus morhua, AMNH 59030.

Urophycis chuss, AMNH 40698, Reynolds Channel by Beach 13th

St. Far Rockaway, Queens, New York, 1 C&S specimen.

Microgadus tomcod, AMNH 36595, Ashoroken Town Beach, Suffolk

Co., New York, 12 C&S.

M. tomcod, AMNH 1084.

Fundulidae

Fundulus heteroclitus, AMNH 28518.

Atherinidae

Atherina temniucki, AMNH 19879, Celebes.

Menidia beryllina, AMNH 35721SW, Dauphin Island Bay,
Alabama.

Menidia menidia, AMNH 40696, Reynolds Channel, Far Rockaway,
New York, 10.

Bedotiidae

Bedotia geayi, AMNH 28132, Riambola River, Tamatave Prov.,
Malagasy, 2 C&S.

Rheocles sikorae, AMNH 28127SW, Manambola River, Tamatave
Prov., Malagasy, 1 C&S specimen.

Trachichthyidae

Hoplostethus mediterraneus, AMNH 49718SW, 33°59'N, 79°05'W

H. mediterraneus, AMNH 49700.

Gephyroberyx philippinus, AMNH 49701SW, Philippines,
8°45'30"N, 123°33'45"E, 1 C&S.

Berycidae

Beryx splendens, AMNH 095737SD, Port Phillip Bay and Bass
Strait (Melborne Fish Market).

B. splendens, AMNH 3555, Tokyo Market.

B. splendens, AMNH 71267, Tokyo.

Holocentridae

Holocentrus ascensionis, AMNH 23663, Great Egg Island,
Bahamas.

Holocentrus marianus, AMNH 23376SW, San Salvador Reef,
Graham's Harbor, Bahamas.

Myripristis jacobus, AMNH 23380, San Salvador Reef, Graham's

Harbour, Bahamas, 1 C&S.

Myripristis murdjan, AMNH 14809SW, Bali, 1 C&S.

Polymixiidae

Polymixia lowei, AMNH 37335, 39°44'N, 72°53'W, 3.

P. lowei, AMNH 49674SW, Oregon, 4 C&S.

Melamphaidae

Scopeloberyx sp., AMNH 49710SW, 2 C&S.

Zeidae

Zeus japonicus, AMNH 894, Japan, 1 C&S.

Z. japonicus, AMNH 52097, Japan.

Zeus faber, AMNH 29458SW, Mediterranean, Gulf of Tunis,
36°50N, 10° 15'E, 1 C&S.

Caproidae

Capros aper, AMNH 51498SW, Mediterranean, 35°41'-35°35'N,
05°12'30"-05°07'40"W, 2 C&S.

C. aper, AMNH 51498.

Hypoptychidae

Hypoptychus dybowskii, USNM 051494, Mauka, Saghalin Is., Sea
of Okhotsk.

H. dybowskii, CAS 41592, NW and Central Pacific, Japan, 2, 1
C&S.

Gasterosteidae

Apeltes quadracus, uncat, Herring Creek, Gayhead, Martha's
Vineyard, 3 C&S.

A. quadracus, uncat, West River, New Haven, Connecticut, 3
C&S.

Pungitius pungitius, uncat, West River, New Haven, 2 C&S
Connecticut.

Scorpaenidae

Scorpaenodes xyris, AMNH 16092, Pearl Island, Sabogo Island,
Gulf of Panama, Pacific, 5 C&S.

Scorpaenodes caribbaeus, AMNH 23114, Dolphin's Head, Cat
Island, Bahamas, 3 C&S.

Acropomatidae

Acropomus japonicum, AMNH 34913.

Ambassidae

Ambassis urotaenia, AMNH 88042.

Percichthyidae

Coreoperca kawamebari, AMNH 34916.

Dicentrarchus labrax, AMNH 32857.

Doderleinia berycoides, AMNH 34800.

Lateolabrax japonicus, AMNH 37028.

Macquaria australasica, AMS 15794-003.

Morone americanus, AMNH 27414SW, No data, 1 C&S.

Morone saxatilis, AMNH 22567SD, no data.

M. saxatilis, AMNH 56499SD, Warms Springs Hatchery, Georgia.

M. saxatilis, AMNH 51028, San Francisco Bay, 10.

Niphon spinosus, AMNH 03970.

Percichthys trucha, AMNH 970.

Polyprion americanus, AMNH 1827.

Stereolepis ischinagi, AMNH 4488.

Synagrops spinosa, AMNH 083293.

Pseudochromidae

Labracinus lineatus, AMNH 31451, Western Australia.

Pseudoplesiops rosae, AMNH 50192, Great Barrier Reef.

Pseudoplesiops typus, AMNH 49638, Kabaena Island.

Plesiopidae

Plesiops melas, AMNH 14926, Bali, 2.

Apogonidae

Apogon binotatus, AMNH 23388, San Salvador, Graham's Harbor,
Bahamas, 9.

Apogon rueppelli, AMNH 31441.

Apogonichthys stellatus, AMNH 8069, Florida.

Astrapogon puncticulatus, AMNH 28175.

Cheilodipterus macrodon, AMNH 50536.

Epigonus pandionis, AMNH 37325.

Gymnapogon sp., AMNH 33780.

Paramia quinquelineata, AMNH 50532.

Phaeoptyx conklini, AMNH 74107.

Pseudamia gelatinosa, AMNH 33691.

Siphamia fuscolineata, AMNH 33749.

Malacanthidae

Malacanthus plumerii, Uncat, Carrie Bow Cay, Between Twin
and S, Water Cay, Belize, 1 C&S.

Lactariidae

Lactarius lactarius, AMNH 32522.

Pomatomidae

Pomatomus saltatrix, uncat, Gay Head, Massachusetts.

P. saltatrix, AMNH 73770.

P. saltatrix, AMNH 65242, North Carolina.

P. saltatrix, AMNH 75306, Canary Islands.

P. saltatrix, AMNH 9066SD, Gulf of Mexico, scale ventral to
anterior dorsal fin.

Scombrops boops, AMNH 34842.

S. boops, AMNH 26832.

Rachycentridae

Rachycentron canadum, AMNH 73896, South Carolina, 2.

Echeneididae

Echeneis naucrates, AMNH 37113, 2.

Remora sp., AMNH 8549, 2.

Carangidae

Caranx equula, AMNH 34834, Japan: Toba market.

Trachinotus goodei, AMNH 3221.

Trachurus japonicus, AMNH 26826.

Nematistiidae

Nematistius pectoralis, AMNH 237.

Coryphaenidae

Coryphaena hippurus, AMNH 15901.

C. hippurus, AMNH 17821.

Menidae

Mene maculata, AMNH 16490.

Leiognathidae

Gazza equulaeformis, AMNH 8171.

Leiognathus equulus, AMNH 88039, Africa, Malagasy.

Sciaenidae

- Aplodinotus grunniens*, AMNH 21018.
- Bairdiella chrysur*a, AMNH 76191.
- Cynoscion nebulosus*, AMNH 084162.
- Cynoscion arenarius*, AMNH 57673SD.
- Equetus* sp., AMNH 085231.
- Genyonemus lineatus*, AMNH 51332.
- Isopisthus parvipinni*, AMNH 20764, 3 C&S, Atafona, State
of Rio de Janeiro, Brazil
- Larimus fasciatus*, AMNH 16295.
- Leiostomus xanthurus*, AMNH 35725SW, Dauphine Island Bay, NE
Shore, Mobile Co., Alabama, 1 C&S.
- Menticirrhus saxatilis*, AMNH 74191.
- Micropogon furnieri*, AMNH 17921.
- Micropogon undulatus*, AMNH 35723SW, Dauphin Island, Mobile
Co., Alabama, 1 C&S.
- Micropogonias undulatus*, AMNH 63986.
- Ophioscion punctatissimus*, AMNH 083649.
- Otolithes argenteus*, AMNH 32545.
- Sciaena trewavasae*, AMNH 33469.
- Seriphus politus*, AMNH 2695.
- Stellifer lanceolatus*, AMNH 76720.
- Umbrina roncador*, AMNH 5545.

Pempherididae

- Pempheris schomburgki*, AMNH 36628.
- P. schomburgki*, AMNH 73546, Central America, Mulatas

Archipelago.

Bathyclupeidae

Bathyclupea argentea, AMNH 49675.

Ephippididae

Chaetodipterus faber, AMNH 085053.

Drepane punctata, AMNH 15888.

Ephippus orzbis, AMNH 18333.

Platax teira, AMNH 50135.

Enoplosidae

Enoplosus armatus, AMNH 48792.

Cirrhitidae

Amblycirrhitus pinas, AMNH 24129.

Cirrhitichthys corallicola, AMNH 16024.

Cirrhitus rivulatus, AMNH 55341.

Paracirrhites arcatus, AMNH 72608.

Chironemidae

Threpterus maculosus, AMNH 31317.

Cheilodactylidae

Cheilodactylus variegatus, AMNH 7269.

Chirodactylus sp. AMNH 37640, Cape Freycinet, W. Australia.

Cepolidae

Acanthocepola kraeseusternii, AMNH 12998.

Cepola rubescens, AMNH 49647.

Opisthognathidae

Opisthognathus maxillosus, AMNH 23435SW, San Salvador,

Bahamas.

O. maxillosus, AMNH 21323.

Congrogadidae

Blennodesmus scapularis, AMNH 49649.

Congrogadus sp., AMNH 37651.

Haliophis guttatus, AMNH 49657.

Mastacembelidae

Mastacembelis congicus, AMNH 6042SW, Stanleyville, Congo, 3
C&S.

Mastacembelis sinensis, AMNH 11078SW, Ho Kán, Kiangsi Prov.,
China, 3 C&S.

Mastacembalis erythrotaenia, AMNH 43433SW, Indonesia, 1 C&S.

Scaridae

Scarus bowersi, AMNH 38114SW, 1, Philipines.

Sparisoma rubripinne, AMNH 15483SW, Boot Key, Monroe Co.,
Florida, 2 C&S.

Cryptotomus roseus, AMNH 31297SW, Bahamas, 2 C&S.

Zoarcidae

Lycodes pallidus, AMNH 20128, Troms. Co., Tranøy Distr.,
Dragøy, Eidsfjord, Norway, 2 C&S.

***incertae sedis* genera**

Siniperca chuatsi, AMNH 37032.

Trachinoidei

Letoscopidae

Leptoscopus macropygus, USNM 213490, New Zealand.

L. macropygus, AMNH 49655.

Champsodontidae

Champsodon USNM 245331.

Champsodon curtipes, AMNH 49666SW, South Channel to Manilla Bay, Philippines, 1 C&S.

Trichonotidae

Trichonotops mutistriatus, ZMH 5349 (Paratype), 12°36'N, 43°16'E.

Trichonotops spec.(I), ZMH 5320, East Coast of Somalia, 1, 1 C&S.

Trichonotops spec.(II), ZMH 5321, 150 Nautical Mile NE of Mogadiscio, Somalia, 2, 3 C&S.

Creedidae

Limnichthys fasciatus, AMNH 57282, Cape Freycinet, Western Australia, 2, 13 C&S.

Crystallodytes cookei, AMNH 51740, Point 1.25 mi South of Fare, Society Islands, French Polynesia, 4, 1 C&S.

Uranoscopidae

Uranoscopus, AMNH 96242SD, New South Wales, Australia.

Uranoscopus japonicus, AMNH 26861SW, Misaki, Japan, 1 C&S.

U. japonicus, AMNH 34892, Mikawa Bay, Japan.

Uranoscopus scaber AMNH 22233SD Italy.

U. scaber AMNH 2945, Market, Naples, Italy. 2.

Uranoscopus asper AMNH 22238SD, Japan.

Astroscopus guttatus, AMNH 70521SW, Virginia Beach, Seashore State Park, Virginia.

A. guttatus, AMNH 17043SW, Coney Island, New York.

Astroscopus y-graecum, AMNH 5772SD, Gulf of Mexico.

A. y-graecum, AMNH 33548, Port Aransas, Aransas Pass, Texas.

A. y-graecum, AMNH 73864, North Inlet, Crabnet Creek, South Carolina.

Kathetostoma cubana, AMNH 49656SW, Leeward Islands, 17°27'N, 62°04'W, 2.

Kathetostoma canaster, AMNH 91942SD, Port Phillip Bay and Bass Strait, Melbourne Fish Market, Australia, 2.

Kathetostoma laeve, AMNH 095348SD, Port Phillip Bay and Bass Strait, Melbourne Fish Market, Australia.

Trachinidae

Trachinus vipera, AMNH 4531SW, no data, 2.

T. vipera, AMNH 49662, Lebanon, St. George Bay, Mediterranean.

Trachinus draco, AMNH 20463SW, Black Sea, Rumania, 2.

T. draco, AMNH 55140, Two Km. off coast of Alicante, Spain.

T. draco, AMNH 17301, no data.

Percophidae

Bembrops anatrostris, AMNH 083323, Gulf of Mexico, 2.

Pinguipedidae

Pinguipes chilensis, AMNH 7292.

Cheimarrichthyidae

Cheimarrichthys fosteri, AMNH 98274, Ashley River, New Zealand, 8, 2 C&S.

Ammodytidae

Ammodytes sp., Lat. 40°55'N, Long. 69°06'W (15 km S of Shinecock), 10, 1 C&S, larvae.

- Ammodytes* sp., Lat. 35°41'N, Long. 74°58'W (60km. N.E. Cape Hatteras), 10, 6 C&S, larvae.
- Ammodytes* sp., Lat. 41°30'N, Long. 67°41'W (200km E. of Cape Cod), 4 6 C&S, larvae.
- Ammodytes* sp., Lat. 41°20'N, Long. 71°21'W (Mouth Naragansett Bay), 2 6 C&S, larvae.
- Ammodytes* sp., Lat. 42°06'N, Long. 67°21'W (220km NE. of Provincetown), 2, larvae.
- Ammodytes* sp., Lat. 41°00'N, Long. 68°44'W (115km E. Nantucket), 2, larvae.
- Ammodytes dubius*, USNM 302239, Lat. 38°47-48'N, Long. 73°15-13'W, 3.
- A. dubius*, USNM 302240, Lat. 41°38'N, Long. 68°27'W, 3.
- A. dubius*, USNM 302232, Lat. 39°24-25'N, Long. 73°26-29'W, 3.
- A. dubius*, USNM 302235, Lat. 39°23-24'N, Long. 73°43-42'W, 3.
- A. dubius*, USNM 165263, Lat. 53°43', Long. 56°59'W, Labrador, Pack's Harbor, 3.
- A. dubius*, USNM 302233, Lat. 38°47-49'N, Long. 74°08-09'W, 3.
- A. dubius*, USNM 302246, Lat. 41°35'N, Long. 69°56'W, 3.
- A. dubius*, USNM 302250, Lat. 41°33'N, Long. 67°58'W, 3.
- A. dubius*, USNM 302238 Lat. 36°46-47'N Long. 75°24-22'W, 1, 2 C&S.
- A. dubius*, USNM 302239, Lat. 38°47-48'N, Long. 73°15-13', 3.

- A. dubius*, USNM 302258, Lat. 41°28'N, Long. 67°46'W, 3.
- A. dubius*, USNM 302242, Lat. 40°59'N, Long. 69°26-28'W, 3.
- A. dubius*, USNM 302247, Lat. 41°21'N, Long. 67°26'W, 3.
- A. dubius*, USNM 302241, Lat. 41°40'N, Long. 69°54'W, 1, 2
C&S.
- A. dubius*, USNM 302248, Lat 41°, 51'N., Long. 70°29'W, 3.
- A. dubius*, USNM 302257, Lat. 41°18'N, Long. 70°28'W, 18.
- A. dubius*, USNM 302252, Chappaquiddick Beach, Martha's
Vineyard, Massachusetts, 2.
- A. dubius*, USNM 303472, Lat. 41°09'N, Long. 68°03'W, 2.
- A. dubius*, USNM 302469, Lat. 40°59'N, Long. 68°19'W, 2.
- A. dubius*, AMNH 20641, Western Bank, Grand Banks.
- A. dubius*, AMNH 59352, Rockaway Inlet, Off Breezy Point,
New York, 8.
- A. dubius*, uncat, Georges Bank, Lat. 41°3.74'N, Long.
68°3.92'W, 2, 3 C&S.
- Ammodytes americanus*, USNM 083720, Truro, Massachusetts, 3.
- A. americanus*, USNM 302253, Chappaquiddick Beach, Martha's
Vineyard, Massachusetts, 3.
- A. americanus*, USNM 036925, Bass Rocks, Gloucester,
Massachusetts, 3.
- A. americanus*, USNM 165371, Mouthof Tessiujarsuk near Nain,
Labrador, 2.
- A. americanus*, USNM 132092, Wood Island, Maine, 3.
- A. americanus*, USNM 302256, Lat. 41°18'N, Long. 70°28', 3.
- A. americanus*, USNM 302255, Nahant, East Point,

- Massachusetts, 3.
- A. *americanus*, AMNH 20792, Gardner's Is., Bostwick Pond, Outlet, Suffolk County, New York, 6 C&S.
- A. *americanus*, AMNH uncat, Isolated Lagoon, Fire Isl. Inlet, New York, 19 C&S.
- A. *americanus*, AMNH 33553, Fire Island Inlet Near Democrat Point.
- A. *americanus*, AMNH 50471, Lat. 36°35'N, Long. 75°46'W, 4.
- A. *americanus*, AMNH 36496, Jones Beach Inlet, W. of Fishing Pier, Nassau County, New York, 19, 8 C&S.
- A. *americanus*, AMNH 36594, Ashoroken Town Beach, Suffolk County, New York, 22 C&S.
- A. *americanus*, AMNH 36514, Robert Moses, Nassau County, New York, 34 C&S.
- A. *americanus*, AMNH 37812, Long Island Sound, Beach E. of Flax Pond Jetties, Suffolk County, New York, Lat. 48°58'N, Long. 73°8.3'W, 20, 12 C&S.
- A. *americanus*, AMNH 36780, Gardner's Island, Bostwick Pond Tidal Gut, Suffolk County, New York, 12 C&S.
- A. *americanus*, AMNH 37813, Far Rockaway, Long Island, New York, 8.
- A. *americanus*, uncat Philbin Beach, Gay Head, Mass., 1 C&S.
- A. *americanus*, Lat. 40°49' Long. 72°08' (80km S.E. Nantucket), 10, 7 C&S, larvae.
- A. *americanus*, Lat. 37°15' Long. 75°31' (50km N.E. Mouth Chesapeake), 2, larvae.

- A. americanus*, Lat. 40°07' Long. 73°44' (50km S.E. Sandy Hook), 5.
- A. americanus*, Lat. 38°43' Long. 73°04' (160km E. Cape May), 5, 2 C&S.
- A. americanus*, AMNH 115140, River Mile 17, Hudson River, New York, 3, 1 C&S.
- A. americanus*, AMNH 115236, River Mile 29, Hudson River, New York, 1, larvae.
- A. americanus*, AMNH 123166, River Mile 34, Hudson River, New York, 2, larvae.
- A. americanus*, AMNH 115162, River Mile 15, Hudson River, New York, 1, larvae.
- A. americanus*, AMNH 115161, River Mile 24, Hudson River, New York, 2, 1 C&S, larvae.
- Ammodytes tobianus*, BMNH 1962.7.30:412-445, Beach Seine, Port Erin Bay, Isle of Man, Great Britain, 1, 5 C&S.
- A. tobianus*, AMNH 58638 (ZMB 25874), Coast of Baltic Sea Near Rostock-Warnemunde, 5, 4 C&S.
- A. tobianus*, AMNH 58640 (NHRM SOK/1987282.5704), Skagerrak, Stora Kornö Island, Smalsund Strait, Sweden, 3, 2 C&S.
- A. tobianus*, AMNH 13285, Dornoch, Firth, Sutherland, Scotland.
- A. tobianus*, AMNH 13284, Dornoch, Firth, Sutherland, Scotland, 3.
- A. tobianus*, AMNH 36831, (Misidentified as *A. marinus*), East Sussex, Brighton, Great Britain.

- A. tobianus*, AMNH, No Data Europe? 2.
- Ammodytes marinus*, (Misidentified as *G. semisquamatus*, DAFS,
Whiten Head, N. Scotland, 5, 4 C&S.
- A. marinus*, BMNH 1985.12.2:26-45, Bamburg Beach, 2, 4 C&S.
- A. marinus*, AMNH 75358, Western North Atlantic Ocean, 9.
- A. marinus*, AMNH 1159 (Misidentified as *A. tobianus*), No
Data, Europe?
- A. marinus*, AMNH 58267, Northern Kattegat Strait, Denmark,
6, 4 C&S.
- Ammodytes personatus*, AMNH 16700, Dutch Harbor, Amaknak
Island, Fox Islands, Alaska.
- A. personatus*, AMNH 3049, No data.
- A. personatus*, RINPF uncat, Mie, Ise Bay, No. 3, Japan, 135,
10 C&S.
- A. personatus*, RINPF uncat, Wakkanai, Hakodate, No. 2,
Japan, 44, 4 C&S.
- A. personatus*, USNM 59498, Prince Wales Island, 2 C&S.
- A. personatus*, USNM 32482, Kodiak, Alaska, 2 C&S.
- A. personatus*, USNM 53930, Bering Sea, 2 C&S.
- A. personatus*, USNM 104499, Nook Bay, Alaska, 2 C&S.
- A. personatus*, USNM 71417, Hakodate, Japan, 1 C&S.
- A. personatus*, USNM 53928, Unalaska, 2 C&S.
- A. tobianus personatus*, UW 4248, Kodiak Island, Alitak, Lazy
Bay, Alaska, 1 C&S.
- A. tobianus personatus*, UW 2106, Puget Sound, San Juan
Island, Friday Harbor, 2 C&S.

- A. tobianus personatus*, UW 6014, Puget Sound, Golden Gardens, Seattle, 1, 2 C&S.
- Ammodytes hexapterus*, UAM 7565, Lat. 71°02'N, Long. 158°32'W, Chukchi Sea, Pt. Barrow, Alaska, 2 C&S.
- A. hexapterus* Qingdao, China 12, 4 C&S.
- A. hexapterus*, UAM 2393, Gambell, St. Lawrence Island, Alaska, 2 C&S.
- A. hexapterus*, UAM 2877, Lat. 64°29.2'N, Long. 167°18.1'W, NE Bering Sea, 2 C&S.
- A. hexapterus*, UAM 3027, Lat. 55°19'N, Long. 130°54'W, Smeaton Bay, Alaska, 2 C&S.
- A. hexapterus*, UAM 1143, Glacier Bay National Monument, Alaska, 2 C&S.
- A. hexapterus*, UW uncat, San Juan Is., Eagle Cove, Puget Sound, 2, 1 C&S.
- A. hexapterus*, UW uncat, Aleutian, Adax Island, Clam Lagoon, 1, 1 C&S.
- A. hexapterus*, UW 17256, Lat. 52°58'N, Long. 179°20'W, 3 C&S, larvae.
- A. hexapterus*, uncat, Pacific NW, Washington, 1, 2 C&S.
- A. hexapterus*, Chilkat River, Lynn Canal, Haines Alaska, 1, 1 C&S.
- A. hexapterus*, RINPF uncat, Wakkanai No.1, 46, 4 C&S.
- A. hexapterus*, AMNH 02712, San Juan Island, Puget Sound, 10.
- A. hexapterus*, AMNH 18779, Bering Strait.
- Ammodytes vittatus*, AMNH 787, Coney Island, New York.

- Ammodytes alascanus*, AMNH 17222, Dutch Harbor, Aleutians,
Alaska.
- Hyperoplus lanceolatus*, AMNH 58639, (NHRM SOK/1987282.5734),
Stora Kornö Island, Smalsund Strait, Sweden, 1, 1 C&S.
- H. lanceolatus*, BMNH 1962.7.30:339-376, Port Erin Bay, Isle
of Man, 2, 4 C&S.
- H. lanceolatus*, AMNH 58266, Inner Danish Waters, 6, 4 C&S.
- Hyperoplus immaculatus*, BMNH 1983.3.8:161-166, Plymouth
Area, 3, 4 C&S.
- Gymnammodytes cicerellus*, AMNH 98276 (from ICM), NW
Mediterranean, Blanes, Spain, 4, 2 C&S .
- G. cicerellus*, USNM 108813, 1 C&S.
- Gymnammodytes capensis*, RUSI 2789, East Cape Province, South
Africa.
- Gymnammodytes semisquamatus*, BMNH 1962.7.30:508-520, Pt.
Erin Bay, Isle of Man, 2, 4 C&S.
- G. semisquamatus*, AMNH 98275 (from ICM), 3 2 C&S, NW
Mediterranean, Blanes, Spain, 3, 2 C&S.
- G. semisquamatus*, DAFS uncat, (Wrongly Identified as *A.
marinus*) Voe, Shetland, Scotland, 2, 2 C&S.
- Bleekeria* sp., BPBM 16949, (misidentified as *Ammodytes*
because scales strongly suggest *Bleekeria* or
Ammodytoides sensu Duncker and Mohr, 1939; Ida and
Randall 1993), Pitcairn Island, Pacific, 10.
- Bleekeria* sp. BPBM 16660, (misidentified as *Ammodytes*
because scales strongly suggest *Bleekeria* or

- Ammodytoides* sensu Duncker and Mohr, 1939; Ida and Randall 1993), Spewings from a carangid, West Harbor, Pitcairn Island.
- Bleekeria* sp. USNM 36514, (misidentified as *Ammodytes* because scales strongly suggest *Bleekeria* or *Ammodytoides* sensu Duncker and Mohr, 1939; Ida and Randall 1993), Hawaii.
- Bleekeria gilli*, CAS 06881, (paratypes of *A. leucasanus*, a junior synonym of *B. gilli*, Collette, MS), Black Beach Anchorage, Charles Island, Galapagoes.
- Bleekeria gilli*, CAS-SU 46501, (paratypes of *A. leucasanus*, a junior synonym of *B. gilli*, Collette, MS), no data.
- B. gilli*, CAS-SU 46502, (paratypes of *A. leucasanus*, a junior synonym of *B. gilli*, Collette, MS), no data.
- B. gilli*, AMNH 16044, Ecuador, 01°07'N, 79°53'W.
- Bleekeria rennei*, RUSI 22986, West Beach, Port Alfred, South Africa.
- B. rennei* ROM 3915, Photos.
- Bleekeria viridianguilla*, CSIRO B.3861, (Junior synonym of *Herklotsina viridianguilla*, Collette, pers. comm.) 19°05'S-19°06'S, 120°31'E-120°30'E, scale - 137mm and 143mm, 2.
- Herklotsina viridianguilla*, ANSP 53462-53465, Hong Kong.
- Embolichthys mitsukurii*, AMNH 77850, Taiwan, 10, 9 C&S.
- E. mitsukurii*, CSIRO B.3585, 19°31.2'S-19°30.0'S, 116°02.5'E-116°01.9'E, 2.
- E. mitsukurii*, USNM 59599, 2.

Embolichthys sarisa, ANSP 113091, 13°11.2'N, 61°05.3'W.

Character Survey

The following characters are surveyed for this phylogenetic investigation of Ammodytidae. Apomorphies are given in bold after character numbers and absence of the condition is assumed to plesiomorphic unless plesiomorphic state is discussed in the description. Individual states are explained in detail for multi-state characters with the most apomorphic state described in bold after character number.

Lepidology: Characters 1-7

Ornamentation of the acanthomorph scale plate is characterized by well defined regions or fields. A suite of characters representing the fields are used to describe complex lepidologies that are otherwise ignored if scales are characterized by one generalized term such as cycloid or ctenoid. This coding scheme is based upon the assumption that individual fields are interpretable as independent units of evolutionary transformation. The great diversity encountered in multi-field scales, especially the posterior field (McCully 1961, Hughes 1981, Lanzig and Higginbotham 1974, Roberts 1993, Figs. 22, 24, 25, 26) helps justify this premise. Polarization and ordering of scale field character transformation series come from observations made on adults,

juveniles, regenerated scales, accessory scales and mapping character states on cladograms depicting hypotheses of fish interrelationships (Rosen 1973 1985, Johnson 1992, Stiassny 1984, Johnson and Patterson 1993, Fig. 2a).

Scale variation is described by a multi character complex representing the anterior field (character 1), posterior field (character 2), lateral field (character 3), focus or nucleus (character 4) and shape (character 5). This coding scheme is flexible and can be applied to any teleostean scale, even cycloid scales which exhibit minimal field demarcation. For example, a plesiomorphic cycloid scale is round or oval, has numerous concentric ridges around a central focus and lacks sulci, radial ridges, scalelets and field definition. Concentric ridges in any field, round shape and round nucleus defined by a continuous concentric ridge are plesiomorphic. Therefore, a primitive cycloid scale would have states (0) for characters 1-5.

Less derived teleosts such as *Parasudus* (Fig. 29) or salmonids (Järvi and Menzies 1936) have scales which are usually described as cycloid but careful appraisal sometimes reveals presence of subtle structural detail which can also be represented by the five scale character system. For example, *Parasudis* (Fig. 29) is coded with state (0) (concentric ridges) for characters 2, 3 (posterior field, lateral field) and character 4 (nucleus). However, more derived morphologies are apparent in the anterior field and

shape so state (1) (concentric ridges with some folding) is used for character 1 (anterior field) and state (1) (some angularization of shape) for character 5 (scale shape). In another example illustrating this coding system, scales of *Trachinus* (Fig. 10) have state (2) for character 1 (five or more anterior field scalelets) and state (0) for character 2 (concentric ridges in posterior field), character 3 (concentric ridges in lateral field), character 4 (round nucleus with no ornamentation) and character 5 (round shape).

Character 1: Morphology of anterior field. Wide gap between anterior field scalelets comprised of low radial ridge extending from focus to anterior margin (Fig. 11, **AFRR**). Within ctenosquamates (*sensu* Rosen 1973), scales with less than five anterior field scalelets separated by sulci, first appear in myctophids (Fig. 41, **AFS**). Ridges (Fig. 70, **AFSR**) in the scalelets end at the sulcus and do not cross into the next scalelet. Five or more anterior field scalelets (Fig. 12, **AFS**) separated by well defined sulci (Fig. 12, **SUL**) are typically observed in atherinomorphs (Hollander 1986), mugilids (Liu and Shen 1991), perciforms (Coburn and Gaglione 1992, Hughes 1981, Lanzig and Higginbotham 1974, McCully 1960) and ammodytids (Figs. 11, 12).

At the phylogenetic level of Ammodytidae, greater than five primary anterior field scalelets and sulci is

plesiomorphic since all members of the outgroup have this state. Sulci are observed in *Embolichthys* (Fig. 12) and *Bleekeria* (Figs. 70-72). Other genera (Figs. 11, 73, 74, 86, 95) show a somewhat different feature separating anterior field scalelets. Instead of sulci, they exhibit relatively wide gaps comprised of tubular-like ridges, originating in the nucleus and ending at the anterior margin. These structures require some new terminology and are designated **anterior field radial ridges** (AFRR, Fig. 11). Anterior field radial ridges are specializations unique to *Ammodytes*, *Hyperoplus* and *Gymnammodytes*.

Character 2: Morphology of the posterior field. Radial ridges ending as blunt spines on the posterior scale field margin (Figs. 96, 97, PFRR). The unique sculpting of ammodytid posterior scale fields has never been explicitly characterized. Descriptions of their scales as cycloid completely ignored lepidologies of marginal blunt spines and radially aligned secondary ridges. On the posterior field of *E. mitsukurii* or *B. viridianguilla* (Figs. 12, 16, 70, 96) short perpendicular spurs (Fig. 16, SP) originate from concentric ridges. Away from the posterior margin they appear as spines whose tips are truncated by the next more posterior concentric ridge. These truncated spines look like secondary ridges, except that radial alignment is an important aspect of their morphology, as is continuity with spines on the posterior margin (Fig. 16, spine). Therefore,

new terminology is used for these ridges and they are designated **posterior field radial ridges** (Fig. 96, **PFRR**). Posterior field morphology of *Ammodytes*, *Hyperoplus* and *Gymnammodytes* is similar to *E. mitsukurii* or *B. viridianguilla* (Figs. 11, 73-77).

Scales of other species in genus *Bleekeria* have a slightly different pattern. The posterior field has contiguous rod-like radials underlying concentric ridges and nodules are formed where they cross, a feature first noted by Günther (1862) (Figs. 71, 72). However, these radial ridges could be interpreted in the same way as those of *E. mitsukurii* (Fig. 17), except there is greater continuity which obscures their origin as amputated radially aligned spines.

Radial and concentric ridges in the posterior field of *Trichonotops* (Figs. 13, 97) resembles those of *B. renniei* and *B. gilli* (Figs. 71, 72) more than *E. mitsukurii* or *B. viridianguilla* (Figs. 12, 70, 96). Posterior field radial ridges of *Trichonotops* do not appear to arise from truncated spines but are components of a relatively flat network of radial and concentric ridges. Nevertheless, except for secondary scalelets (Figs 13, 97, **SSP**) in middle of the posterior field, radial ridges of trichonotids appear homologous to those of ammodytids because they are radially aligned and end as blunt spines on the posterior margin.

Liu and Shen (1991, figs. 6C, 8A, 11A) described

membranous cteni in mugilids and similar structures also occur in the enigmatic ammodytid, *Embolichthys sarisa* (Fig. 58). Overall similarity of the membranous cteni from *E. sarisa* with those of some mugilid fishes is striking but difficult to interpret because of marked differences in other aspects of scale morphology. Mugilids have a longitudinal groove at the focus and a grainy pie shaped wedge of ossified matrix beneath the membranous cteni with its vertex abutting the groove (Liu and Shen 1991, figs. 11A, 15C, 16D) while a round simple nucleus and numerous concentric ridges anterior to the membranous cteni are found in *E. sarisa* (Fig. 58).

Three states apply in descriptions of ammodytid and outgroup posterior fields: 1) concentric ridges, 2) lattice of concentric and radial ridges and 3) membranous cteni. Their polarity is somewhat problematic because character states in the outgroup are difficult to interpret and membranous cteni similar to those of *E. sarisa* are found only in mugilids. Uranoscopids and trachinids show concentric ridges but uranoscopid ridges are highly compressed and appear autapomorphic, while trichonotid radial ridges seem homologous with ammodytids. Nevertheless, occurrence of concentric ridges (state 0) is assumed to be plesiomorphic (Fig. 10) because of its widespread distribution in fishes more primitive than the outgroup. State (1) represents posterior fields with

membranous cteni. It is a further derived condition of state (0) because numerous concentric ridges remain in the posterior field (Fig. 58) just anterior to membranous cteni. State (2) describes a marginal concentric ridge with perpendicular blunt spines and network of radially aligned secondary ridges formed as spine tips are truncated by growth of more posterior concentric ridges with accompanying spines. This lepidology is apparently homologous in Ammodytidae (Fig. 16) and Trichonotidae (Fig. 13), despite occurrence of secondary scalelets in middle of trichonotid posterior field (Fig. 13, **SSC**).

Character 3: Morphology of the lateral field.

Secondary ridges arising perpendicularly from concentric ridges (Figs. 96, 97, **LFSR**). Lateral fields have parallel ridges (McCully 1961, Figs. 12, 13, 26) with varying degrees of curvature (Fig. 24) and concentricity. Lateral fields rarely show any other type of ornamentation, except secondary ridges are observed in ammodytids (Figs. 70, 96) and trichonotids (Fig. 97). Ammodytid and trichonotid scales show secondary ridges (**LFSR**) arising perpendicularly from lateral field concentric ridges (**LFCR**) (Figures 96 and 97). Lateral field secondary ridges are similar to those of posterior field radial ridges in their being radially aligned but they do not end on scale margin as spines. The plesiomorphic condition is characterized by concentric ridges tracing an arc around the central focus or ridges

approximately parallel to scales anterior-posterior main axes (Fig. 58). Secondary ridges which arise from lateral field concentric ridges (Figs. 96, 97) are derived.

Character 4: Structure of scale nucleus. Nucleus or focus not defined by a continuous concentric ridge but the anterior half of focus penetrated by convergence of anterior field radial ridges (Figs. 73, 74). The round or oval nuclei of many perciforms, percoids (McCully 1961, figs. 4, 5, 6, 16, 17, Figs. 24-26) and more primitive euteleosteans (*Parasudus* - Fig. 29, salmonids - Järvi and Menzies 1936) are smooth and demarcated by a full concentric ridge. *Embolichthys sarisa* and *Bleekeria* minus *B. viridianguilla* exhibit simple round smooth foci (Figs. 58, 71, 72) bordered by a continuous concentric ridge. *Embolichthys mitsukurii* has some ill defined secondary ridges (Figs. 12, 70, 96) in the nucleus but its nucleus is bounded by a continuous concentric ridge. *Ammodytes*, *Hyperoplus*, *Gymnammodytes* have anterior radial ridges contacting a short amorphous dorso-ventral secondary ridge (Figs. 70, 73-79, 95) in the nucleus. Consequently, the concentric ridge surrounding the focus is perforated by anterior field radial ridges. The primitive state is defined by smooth central portion bordered by continuous concentric ridge (Figs. 58, 71, 72). The derived condition is characterized by convergence of radial ridges from anterior field which (Figs. 70, 73-79, 95) create gaps in concentric ridge surrounding focus.

Character 5: Shape of scale. Transformation of scales from pentagonally shaped to round, oval or ellipsoidal (Figs. 12, 13). Change of scales from primitive cycloid (Järvi and Menzies 1936, Figs. 26, 33, 38) to derived transformed ctenoid McCully 1961, Roberts 1993, Figs. 25, 26) coincides with a shape change from round to pentagonal. The shape change also parallels appearance of anterior field scalelets separated by sulci. As already pointed out some so called cycloid scales (*Parasudas* Fig. 29) show increasing angularity and anterior field folding which is succeeded in more derived groups by pentagonally shaped scales with anterior field scalelets (Figs. 12, 13, 25, 26).

The first obvious pentagonal scales are found on aulopoids, exemplified by *Aulopus* (Fig. 57). Such scales are characterized by parallel lateral margins and a straight anterior margin perpendicular to lateral edges. The posterior boundary is comprised of two edges of equal length meeting at a vertex. A line from this vertex to middle of the anterior margin divides the scale into two approximate symmetrical, mirror image, halves. Variations on this pentagonal pattern are frequently seen in modification and rounding of either one or both the anterior (Figs. 25, 62) or posterior borders (Figs. 51, 60) and degree of parallelism of the lateral edges (Figs. 63, 73-75).

Groups more primitive than Aulopiformes show a rounded cycloid scale without field definition (Fig. 15).

Nevertheless, Ammodytidae rounded or oval scales are considered derived because they retain derived four field lepidologies. Evidence for this polarity assumption can be obtained by comparing scales of the putatively most primitive ammodytid, *Embolichthys* (Fig. 12), to representatives from other genera (Figs. 11, 72-82). *Embolichthys* has pentagonally shaped scales while other ammodytids have round or elliptical scales. Of course a more spherical scale could be interpreted as a reversal but for ammodytids (Figs. 72-74, 76-78) an elliptical shape, retention of four fields and distortion of field symmetry suggests that rounded shapes are apomorphic.

The plesiomorphic state (0), describes scales that have a pentagonal outline with nearly bilateral symmetry. State (1) represents round outlines embodied by scales of *Trachinus* (Fig. 10), *Bleekeria renniei* (Fig. 71) and *Gymnammodytes* (Fig. 95). Elliptical or oval scales, accompanied by expanded dorso-ventral axes, characterize state (2) (Figs. 72-74, 76-78). State (3) denotes rounded scales with retention of some straight margins. Scales of *Hyperoplus*, *Ammodytes marinus*, *A. hexapterus* and *A. personatus* illustrate this condition (Figs. 11, 73-75).

Character 6: Loss of lepidonts on anterior scalelet ridges (Figs. 88-90). Lepidonts or minute tooth like denticles (Fig. 85, **LEP**) are found on ridges of the anterior field ((Fig. 85, **AFSR**) of many perciforms (McCully 1961,

Lanzing and Higginbotham 1974) and poeciliids (Hollander 1986) but also occur on concentric ridges of *Chlorophthalmus* (Fig. 92). Distribution of lepidonts in teleostean fishes has not been extensively studied and therefore polarization of their presence or absence is difficult to assess. The occurrence of lepidonts in *Chlorophthalmus* and their widely disjunct distribution in percomorphs suggests that lepidonts are primitive in perciforms but yet highly plastic. The distribution of lepidonts in trachinoid fishes, as defined by Pietsch and Zebatian (1990), exemplify this plasticity as well. They are absent in most ammodytids, leptoscopids, *Cheimarrichthys*, trachinids and uranoscopids but present in *Embolichthys*, *Bleekeria viridianguilla*, *Trichonotops* (Figs. 93, 94, Fig. 2a, 2b) and greatly reduced in other species of *Bleekeria* (Fig. 87).

Despite the inconsistencies with regard to possession of lepidont in many families and groups, there appears to be a phylogenetically consistent pattern in ammodytids. The putatively most primitive ammodytid (Fig. 2b) has lepidonts (*Embolichthys*, Fig. 83-86) which gives way to lepidont reduction (*Bleekeria*, Fig. 87) and finally loss (*Ammodytes*, *Hyperoplus* and *Gymnammodytes*, Fig. 88-91). The following states characterize the degree of lepidont formation and or loss: state (0) - lepidonts on the ridges of anterior field scalelets, state (1) - reduction in size and number of lepidonts, state (2) - no lepidonts.

Character 7: Scale field symmetry. High degree of field asymmetry is derived relative to symmetric fields (Figs. 80-82). Symmetry of typical percomorph, four field or transformed ctenoid scales are fundamentally bilateral (McCully 1961, Lanzing and Higginbotham 1974, Hughes 1981, Hollander 1986, Figs. 12, 13, 25, 26). *Embolichthys mitsukurii* has many bilaterally symmetrical scales on its body, illustrated by Figure 12 for a scale removed above anal fin. However, flank scales are distorted and there is some rearrangement in the size and shape of individual fields relative to each other (Fig. 68). It thus appears that field symmetry correlates with pentagonal bilateral symmetry. Within Ammodytidae, scales which change shape from pentagonal undergo a simultaneous increased amount of field asymmetry even if the scales themselves are bilaterally symmetric (Figs. 77, 80-81). For example, greater distortion in field symmetry becomes apparent by examining the following scales in this order using *Embolichthys* (Fig. 12) as a reference: *Bleekeria viridianguilla* (Fig. 70), *E. mitsukurii* flank scale (Fig. 68), *A. hexapterus* (Fig. 75), *A. marinus* (Fig. 11), *A. americanus* (Fig. 77) and *Bleekeria* (Figs. 71, 72, 80-82).

Explanations for such field asymmetry involve only speculation. There are no satisfactory reasons why the smaller of two lateral fields is always the dorsal lateral field. Perhaps one way of interpreting this asymmetry is by

postulating a clockwise radial shift of the fields accompanied by contraction of dorsal lateral field and expansion of the ventral lateral field (Figs. 73-76). The developmental reality may not be in agreement with this explanation but apparent shifts in lateral field symmetry could be due, at least in those taxa with plicae, to scales assuming a more perpendicular orientation to oblique rows. Shape and size changes of anterior and posterior fields thus seem more conservative while the more plastic lateral fields change with angle of the oblique row (Fig. 69). However, high degrees of field asymmetry observed for scales of *Bleekeria* is perplexing since they have overlapping scales which do not exhibit any shift from the typical anterior - posterior orientation. In some species of *Bleekeria* the asymmetry is extreme with ventral lateral field overlapping the posterior field and comprising about one quarter of the posterior margin (Figs. 72, 80, 81).

Three states are used to describe scale field symmetry. State (0) is the plesiomorphic condition characterized by well defined field symmetry on a bilaterally symmetric pentagonal scale. State (1) defines those scales which show asymmetry of individual fields but relationship of fields to each other are the same as symmetric field scales. Examples include *A. marinus*, *A. americanus* and *A. dubius* (Figs. 11, 77, 78). State (2) describes distorted field symmetry exhibited by some *Bleekeria* species (Figs. 71, 72) where the

ventral lateral field extends posteriorly, overlapping part of the posterior field.

Character 8: Possession of an elongate, terminal, lateral line scale which juts out over the middle rays of the caudal fin (Figs. 98-101). *Ammodytes*, *Gymnammodytes* and *Hyperoplus* have an elongate, spade-shaped terminal lateral line scale at the base of the caudal fin. The scale's blunt rounded anterior margin is even with the posterior end of hypural plate and its sharper posterior tip juts out over middle rays of caudal fin. This elongate caudal scale is an extension of the lateral line and it has an open perforated groove bisecting it longitudinally (Fig. 20). *Hyperoplus* (Fig. 101) sometimes shows a smaller satellite scale posterior to the prolonged larger one. Reay (1986) pictured one on *Ammodytes tobianus* but did not discuss its phylogenetic significance. *Trichonotops* and *Leptoscopus macropygus* also have similarly extended terminal lateral line scales in the same position, except they exhibit tubular roofed canals instead of open grooves and their scales are much longer than those of Ammodytidae (Figs. 18, 19).

These modification of the terminal lateral line scale can be characterized by a multistate character. Absence of the scale is primitive. Possession of a highly elongate scale with enclosed tubular canal is represented by state (1). State (2), found in all species of *Hyperoplus*,

Gymnammodytes and most species of *Ammodytes*, is characterized by elongate, spade shaped scales with open perforated grooves whose anterior end is markedly wider than the posterior (Figs. 20, 100, 101). Scales with narrower and approximately equal anterior - posterior widths occur on northwest Atlantic *Ammodytes* (Figs. 98, 99) and are represented by state (3).

Character 9: Absence of pelvic fins (Fowler 1931, fig. 13, Smith, 1957, fig. 2). Possession of small pelvic fins was used by Jordan (1903, fig. 1) to characterize the genus *Embolichthys*. Pelvics were also observed on *E. sarisa* by Robins and Böhlke (1970, fig. 1) but they felt that loss of pelvics on other ammodytids are inconsequential. However, other independent data (Robins and Böhlke 1970, Pietsch and Zebatian 1990), suggest that *Embolichthys* is the most primitive member of Ammodytidae and genera without pelvics are phylogenetically derived (Fig 2b). Furthermore, presence of pelvic fins in outgroup families Trichonotidae, Trichinidae and Uranoscopidae supports hypothesis that presence of pelvic fins is primitive for ammodytids and their absence derived.

Character 10: Large oval foramen in dentary (Fig. 110, FOR). Monophyly of Ammodytidae has been well documented by Pietsch and Zebatian (1990) with a number of synapomorphies, one being a large oval foramen in the dentary (Pietsch and Zebatian, 1990, fig. 9).

Character 11: Conspicuous spine like process on metapterygoid (Fig. 129, **MTP**). This character was a second synapomorphy supporting monophyly of Ammodytidae (Pietsch and Zebatian, 1990) and is well documented in all ammodytids (Fig. 129).

Character 12: Anteriorly directed symphysial process on dentary (Figs. 110, 17, **SYMP**). In 1839 Swainson thought that *Ammodytes* was closely related to *Lepidopus* based upon their sharing an extended and pointed lower jaw and continuous dorsal fins without spines. No further investigations were made on homology of their lower jaws or their relationship. Much latter Pietsch and Zebatian (1990, fig. 9) used the anteriorly directed symphysial process on the dentary as a synapomorphy for Ammodytidae (see also Figs. 110, **SYMP**, Fig. 17 radiographs of *E. sarisa* and *G. capensis*, Ida 1973, fig. 1). This is a unique osteological feature and is additional proof that Ammodytidae are monophyletic.

Character 13: Scales in oblique rows with united epidermal covering between scales (Fig. 4b, **PL**). Scales in oblique rows termed plicae (Fig. 4b, **PL**, Reay 1970, Nizinski *et al.* 1990) are observed in two genera of ammodytids, *Ammodytes* and *Hyperoplus* (Fig. 4b). Oblique scale rows with united epidermal covering between scales also occur in trachinids and uranoscopids (Pietsch and Zebatian 1990). Because phylogenetically more primitive ammodytids have

overlapping scales (*Embolichthys* and *Bleekeria*) and *Gymnammodytes* is nearly naked of scales, the occurrence of scales in oblique rows in *Ammodytes* - *Hyperoplus* and Uranoscopidae - Trachinidae is parsimoniously interpreted as independent derivations (Fig. 2b). Overlapping scales are plesiomorphic and widespread in numerous acanthomorphs, trachinoids (Pietsch and Zebatian 1990), trichonotids, *Embolichthys* and *Bleekeria*. State (1) is exemplified by fishes which have scales in oblique rows with united epidermal covering between the scales. Species in the genus *Gymnammodytes* show a marked reduction in body scale coverage with anterior half of body naked and widely dispersed scales on posterior section and caudal peduncle (Fig. 4b). This body scale pattern is represented by state (2).

Character 14: Presence of ventrolateral skin folds (Fig. 4b, **VLSF**). All species of *Ammodytes*, *Hyperoplus* and *Gymnammodytes* possess ventrolateral skin folds (Fig. 4b, **VLSF**). Absence of folds in *Embolichthys*, *Bleekeria* and outgroup indicates that lack of ventrolateral skin folds is plesiomorphic. State (1), observed in the Mediterranean *Gymnammodytes cicerulus* and all other members of genera *Ammodytes* and *Hyperoplus*, finds the fold ending past anterior end of the anal fin. *Gymnammodytes semisquamatus* and *Gymnammodytes capensis* display an abbreviated skin fold, ending just past the tip of pectoral fin which is designated state (2).

Character 15: Complex association of extra cartilages and ossicles in the jaw (Fig. 110). Kayser (1961), Gosline (1963) and Ida (1973, 1976) paid special attention to a unique array of cartilages, ligaments and ossicles in the jaws of ammodytids. Pietsch and Zebatian (1990) used this character as a synapomorphy supporting monophyly of Ammodytidae. Ida (1973) found extra ossicles in oral region of *Bleekeria vaga*, *B. gilli* and *B. renniei* (labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, premaxillo-rostral) were in homologous positions as labial ligaments and cartilages of *Embolichthys mitsukurii* and *Bleekeria viridianguilla* (labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, premaxillo-rostral ligament including cartilage V).

Gymnammodytes has labial ossicles 2 and 6 (Fig. 110, **L6** and **L2**), maxillo-dentary ossicle (Fig. 110, **MD**), maxillo-vomerine ossicle (Fig. 110, **MV**) and one bone comprises maxillo-premaxillary ossicles 1-3 and the lateral maxillo-premaxillary ossicle so that the lateral maxillo-premaxillary ossicle is fused perpendicularly to middle of main maxillo-premaxillary ossicle (Fig. 110, **MPLP-F**). Unlike illustration of Ida (1973, fig. 2), the anterior end of fused maxillo-premaxillary ossicles has two prongs through which premaxillary ascending processes pass. *Gymnammodytes* lacks accessory labial cartilages and

premaxillo-rostral ligament. Ida (1973) found that *Ammodytes hexapterus* shows no ossification for any of these cartilages and it also lacks accessory labial cartilages and premaxillo-rostral ligament.

Arrangement of ossicles and ligaments can be expressed by a five state character: state (0) - no extra labial ossicle or ligaments; state (1) - possession of the following ligaments and cartilages: labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, premaxillo-rostral ligament including cartilage V (Ida 1973); state (2) - Labial ossicles 1-6, accessory labial ossicles 1-4, maxillo-dentary ossicle, maxillo-vomerine ossicle, maxillo-premaxillary ossicles 1-3, lateral maxillo-premaxillary ossicle, prerostal ossicle (Ida 1973); state (3) - labial ossicles 2 and 6, maxillo-dentary ossicle, maxillo-vomerine ossicle (Ida 1973, figs. 2, 3) and maxillo-premaxillary ossicle fused with lateral maxillo-premaxillary ossicle (Fig. 110), absence of accessory labial cartilages and ossicles and premaxillo-rostral ligament, state (4) - same ligaments and cartilages as above state (1) except the maxillo-rostral ligament and accessory labial cartilages are absent.

Character 16: Consecutive arrangement of pharyngobranchials (Figs. 132-137). Rosen (1973) stated that a trend in functional emphasis on anterior pharyngobranchials was seen in Eurypterygii by elongation of

pharyngobranchial 3 and lateral displacement of pharyngobranchial 1 and 2. Sometimes it is difficult to understand how he interpreted lateral displacement as a derived state because examples Rosen used to illustrate the primitive serial arrangement of pharyngobranchials also exhibit lateral displacement of pharyngobranchials 1 and 2 (Rosen 1973, figs. 3, 5, 18, 19). However, careful examination of those figures (Rosen 1973, figs. 4, 14, 20-22) which depict elongation of pharyngobranchial 3 and lateral displacement of pharyngobranchial 1 and 2, reveal that anterior tip of pharyngobranchial 3 is well anterior or almost even with anterior end of pharyngobranchial 2 (Rosen 1973, figs. 69, 95, 97, 104-107). This is also observed on some perciforms illustrated by Rosen and Patterson (1990, figs. 42, 43, 47, 49, 50).

Fink and Weitzman (1982) stated that where the "elongate third pharyngobranchial that displaces the second pharyngobranchial from the midline" does not occur, the lack of displacement is a "neomorphic feature". They cited Rosen's (1973) figure 88 for dorsal gill arches of *Hoplostethus* as an example and some additional examples in percomorphs can be seen in Rosen and Patterson's (1990), figures 38-43. However, an elongate pharyngobranchial 3 which displaces pharyngobranchial 2 from midline, is obviously present in most eurypterygians (Rosen 1973, figs. 4, 6-15, 69-71, 91-97). Fink and Weitzman (1982) did not

argue against using elongation of PB3 and lateral displacement of PB2 as a eurypterygian synapomorphy. Although, the presence of this morphology in some stomiiforms could characterize a slightly more inclusive assemblage including them as well.

Dorsal gill arches of *Embolichthys mitsukurii* show (Figs. 130, 131) a serial arrangement consistent with Rosen's (1973) interpretation of pharyngobranchial morphology from pre-Eurypterygii groups. All other species of ammodytids display another type of serial configuration (Figs. 132-137). Consequently, Rosen's (1973) terminology appears somewhat inaccurate because serial organization of pharyngobranchials would be a better description of the morphology found in *Ammodytes*, *Hyperoplus* or *Gymnammodytes* than his usage of serial (Rosen 1973, figs. 3, 5, 18, 19) where there is lateral displacement of PB2. Rosen's concept of primitive in arrangement of pharyngobranchials would mean that *Ammodytes*, *Hyperoplus* and *Gymnammodytes* have dorsal gill arches with more affinity to those of primitive euteleosteans and *Embolichthys* shares similarities with pre-eurypterygians. This interpretation does not agree with the facts that all ammodytids possess the advanced feature of acanthopterygians (Rosen 1973) by having their retractor arcuum branchialum muscle inserted principally on PB3 and overall plesiomorphy of *Embolichthys* (Figs. 2b, Pietsch and Zebatian 1990) in ammodytid phylogenies. These

incongruities makes more sense if the dorsal gill arches of ammodytids are considered neomorphic which is essentially similar to Fink and Weitzman's (1982) conclusions concerning exceptions to Rosen's pattern of dorsal gill arch morphology. In light of these new findings, the pharyngobranchial morphology of *Embolichthys* (Figs. 130, 131) and outgroup (Fig. 118, 123) is judged primitive relative to the consecutive arrangement exhibited by *Ammodytes*, *Hyperoplus* and *Gymnammodytes* (Figs. 132-137).

Character 17: Absence of scales on caudal fin musculature (Reay 1986, fig. 8, p. 946). Reay (1970, 1986) noted that *A. tobianus* could be distinguished from *Ammodytes marinus* by possession of scales on caudal fin musculature, scales in tight chevrons on ventral surface and scales up to and just anterior to dorsal fin. Scales over musculature at base of caudal fin is primitive since it is ubiquitous on perciforms, trachinoids, *Embolichthys* and *Bleekeria*. Absence of such scales is considered apomorphic and is observed on all species of *Hyperoplus*, *Gymnammodytes* and *Ammodytes* with the exception of *A. tobianus*.

Larval Pigmentation: Characters 18-22

The utility of larval pigmentation for identification of some species of Ammodytidae (Corbin and Vati 1949, Einarsson 1955, Macer 1967, Reay 1970, Scott 1972) prompted

further exploration into their suitability as character data in this analysis. First a list of ammodytid larval pigmentation characters, which effectively separated some species, was compiled. Macer (1967) united *A. marinus*, *A. hexapterus* and *A. dubius* on the basis of sharing the following characters: (1) post-anal ventral body pigment continuing to tip of notochord as caudal pigment, (2) dorsal pigment develops from notochord tip and (3) dorsal pigment lighter and latter in development than *Hyperoplus* species. Much of the information Macer provided was a distillation of previous work by Corbin and Vati (1949). Macer (1967) and Scott (1972) also found (4) ventral fin membrane pigmentation effective in categorizing larval ammodyids. Reay (1970), summarizing data of Einarsson (1955) and Macer (1967), discussed two larval pigmentation features which distinguish *A. tobianus* from *A. marinus*. *Ammodytes marinus* has (5) caudal pigment appearing before length of 15 mm and (6) pre-anal ventral body pigment remaining conspicuous. No caudal pigment before length of 15 mm and pre-anal ventral body pigment rapidly obscured by body wall are alternate states observed in *A. tobianus*.

Characters from those listed above (characters 1-6) were search for in descriptions, tables and drawings from the following literature on larval ammodyids, trachinids, trichonotids and uranoscopids: *Ammodytes* (Cameron 1959, Richards 1982) *Embolichthys* and *Bleekeria* (Leis and Trnski

1989, fig. 655), trachinoids (Watson et al. 1984, tab. 137), trichonotids (Leis and Rennis 1984, fig. 52), uranoscopids (Leis and Trnski 1989, figs. 62, 63), trachinids (Russel 1976, 59, 60). Choice of characters to use were made on the basis of their being relatively easy to find in the literature for most species employed in the study. Subsequent larval pigmentation characters are a synthesis of the literature but basically coincide with those discussed by Macer (1967, pigmentation of ventral fins, dorsal body pigment, ventral body pigment, ventral gut pigment), Reay (1970, caudal pigment before larvae 15mm in length) and Watson et al. (1984 gut pigmentation).

Character 18: Pigmentation of larval ventral fin membranes absent (Cameron 1959, pl. 1, facing p. 24). Ventral fin-membrane was a term applied by Corbin and Vati (1949), Cameron (1959) and Macer (1967) to describe a long larval ventral fin with rays joined by membrane, that spanned the ventral midline from level of pectoral fin to caudal peduncle (Cameron 1959, fig. 1). Later in development this fin is replaced posteriorly by the anal fin. Therefore, in this context ventral fins do not refer to pelvic fins.

Macer (1967) pointed out *Gymnammodytes semisquamatus* was the only ammodytid with larval ventral fin membrane pigmentation and Scott (1972) confirmed its absence in *A. dubius* but Leis and Trnski (1989) showed larger larvae of

B. viridianguilla and *E. mitsukurii* have pigmented ventral fin membranes. Watson *et al.* (1984) listed trichonotids with unpigmented anal fins initially but becoming pigmented with development. Therefore, because ventral pigmentation occurs in some outgroup taxa and primitive ammodytids it is considered primitive. State (0) represents presence of pigment and derived state (1), absence.

Character 19: Presence of larval dorsal body pigmentation (Macer 1967, figs. 2a-d, 3a-d). Macer's (1967) description of dorsal body pigmentation continuing to notochord tip is somewhat difficult to observe on examples from the literature (Richards 1982; Leis and Trnski 1989, fig. 655; Watson *et al.* 1984, tab. 137; Leis and Rennis 1984, fig. 52; Leis and Trnski 1989, figs. 62, 63; Russel 1976, figs. 59, 60). However, Macer noted that highly pigmented dorsal bodies are characteristic of *Hyperoplus* larvae and dorsal pigmentation is easy to see on examples from the literature. Consequently, dorsal pigmentation is utilized as a character. Polarization of the plesiomorphic state is based upon absence of dorsal body pigmentation in trichonotids and trachinids.

Character 20: Ventral body pigmentation of larvae continuing to notochord tip (Macer 1967, figs. 4a, 4b). Pigmentation of ventral body has been well illustrated on most ammodytids and the trachinoid outgroup (Leis and Trnski 1989, fig. 62, 63, 655, Watson *et al.* 1984, tab. 137, Leis

and Rennis 1984, fig. 52, Richards 1982, Russel 1976, figs. 59, 60, Macer 1967, fig. 4a, 4b). Character 20 reflects three states which occur in examples from the literature: (0) - absence of ventral pigment, (1) - ventral pigment present but not continuing to notochord tip and (2) - post anal ventral body pigment continuing to tip of notochord as the caudal pigment. Lack of pigmentation in Trachinidae and Uranoscopidae effectively polarizes this state as primitive.

Character 21: Ventral gut pigmentation present (Macer 1967, figs. 1, 2). Watson's *et al.* (1984, tab. 137) table provided initial data for this character in trachinoids, but ventral gut pigmentation is also easily obtained from other diagrams and descriptions (Leis and Trnski 1989, fig. 62, 63, 655; Leis and Rennis 1984, fig. 52; Richards 1982; Russel 1976, figs. 59, 60; Macer 1967, fig. 4a, 4b). Absence of ventral gut pigmentation in all outgroup taxa indicates that it is plesiomorphic.

Character 22: Caudal pigmentation present on small larvae, less than 15 mm in length. *Ammodytes marinus* shows caudal pigmentation on larvae less than 15 mm in length (Macer 1967, fig. 4) while *A. tobianus* does not. This character was originally used by Reay (1970) to distinguish their larvae but the literature (Leis and Trnski 1989, fig. 62, 63, 655, Watson *et al.* 1984, tab. 137, Leis and Rennis 1984, fig. 52, Richards 1982, Russel 1976, figs. 59, 60, Macer 1967, fig. 4a, 4b) gives good examples of this

pigmentation in other species. Polarization of the primitive state is based upon finding pigmentation absent on larvae less than 15 mm long in trichonotids and trachinids.

Character 23: Highly elongate anterodorsal process of suboperculum (Fig. 112, SOPP). A prominent, elongate, anterodorsal arm of the suboperculum is observed in ammodytids and trichonotids. It extends dorsally toward posterior arm of hyomandibula and borders approximately three quarters of opercular anterior margin. This condition is pictured in Figures 112, 114 (SOPP) and can be contrasted with primitive state, showing a much shorter process, illustrated by Figure 111. The plesiomorphic process usually skirts no more than one third length of anterior opercular margin.

Character 24: Presence of two vomerine fangs and anterior margin of vomer notched (Einarsson 1951, figs. 6, 7). *Hyperoplus* adults possess two large fang-like teeth on the vomer which form a conspicuous notch on vomerine anterior margin. Larvae of *Hyperoplus* and *Gymnammodytes* also display two vomerine teeth but teeth are lost in adults of the latter (Einarsson 1951). Einarsson (1951) studied a size series of postlarvae finding that the anterior tip of the vomer is pointed on *A. tobianus* which has no vomerine teeth in any ontogeny and a median cleft is present on the anterior vomer of *Hyperoplus lanceolatus*. Adults and postlarvae of *Gymnammodytes* also have a pointed anterior

vomerine margin. Thus, homology of larval vomerine teeth for *Hyperoplus* and *Gymnammodytes* is questionable owing to differences in shape of anterior vomer and the role fangs play in formation of anterior notch in *Hyperoplus*. The apomorphic condition describes two prominent fangs on vomer separated by an anterior notch in both larvae and adults. The primitive state is described by absence of fangs in some or all ontogenies and a pointed anterior vomerine margin in all ontogenies.

Character 25: Maxillary medial process broad with medial process perpendicular to maxillary cranial process (Fig. 108, **MXMP, MXCP-MP**). Kayser (1961) conducted a comparative morphological and mechanical analysis of the protrusile jaw of *A. tobianus* and *A. lanceolatus* (= *Hyperoplus lanceolatus*). He found that *A. tobianus* has more protrusile premaxillaries with muscles and cartilage modified accordingly. One feature which may have been adapted for protrusibility is an articulated ascending process of the premaxilla (Kayser 1961). Fish without highly protrusile jaws such as trachinids, uranoscopids (Pietsch 1989, Pietsch and Zebatian 1990) and trichonotids (Nelson 1985, 1986) have rigidly attached ascending processes while ammodytids exhibit articulated processes.

Other characteristics of upper jaw which have relevance to understanding degree of protrusibility, especially the less protrusile jaws of *Hyperoplus*, comes from morphology

of the maxillaries. Osteology of the maxillaries was discussed by Stiassny (1984) and her terminology is used here. The maxillary medial process is broadened in *Hyperoplus* (Fig. 108, **MXMP**) and there is a small medial process (Fig. 108, **MXCP-MP**) on base of the maxillary cranial process (Fig. 108, **MXCP**). All other ammodytids exhibit a narrower maxillary medial process and lack the medial process on the maxillary cranial process (Fig. 109).

Character 26: Nasal organ smooth and egg shaped (Fig. 7). Ida (pers. comm.) pointed out that nasal organs of some ammodytids are highly convoluted with conspicuous lamellae while others are smooth and egg-shaped. Primitively the nasal organ of a typical perciform is highly convoluted with numerous lamellae. Figures 5 and 6 exemplify this condition in *Cheimarrichthys fosterii* and *Embolichthys mitsukurii* respectively, although number of lamellae are reduced in *E. mitsukurii*. Smooth, egg shaped nasal organs found in all species of *Ammodytes*, *Hyperoplus* and *Gymnammodytes* are derived and exemplified by *Ammodytes americanus* (Fig. 7).

Character 27: Diameter of posterior pore of lateral line scale same width as lateral line canal and in contact with posterior margin (Fig. 105). Variation in diameter and placement of line scale canal pores in genera of ammodytids and the scaleless lateral lines of *Gymnammodytes*, demonstrate that lateral line morphology is phylogenetically significant. *Embolichthys* and *B. viridianguilla* have a pore

whose diameter is less than width of canal roof. The pore is more centrally located, well anterior from scale's posterior margin (Fig. 103). Other species of *Bleekeria* also show a smaller pore diameter relative to width of canal, except the opening is displaced posteriorly (Fig. 104). *Ammodytes* and *Hyperoplus* have pores (Fig. 105, LLP) as wide as lateral line scale canal (Fig. 105, LLC) and positioned on the posterior margin. Their pores are separated from the posterior margin by a thin membrane (Figs. 105, 106).

Gymnammodytes has a scaleless lateral line constructed of an alternating system of horizontal and vertical tubules (Fig. 107). In the gap between every horizontal tubules lies a pore which is ventrally displaced and between every other horizontal tubules above the pore there arises a short dorsally directed tubule perpendicular to lateral line horizontal axis. Another pore is located at the dorsal end of this vertical tubule.

A small, anteriorly displaced, lateral line scale canal pore is observed in trachinids, uranoscopids and many perciforms. Trichonotidae have a deep notch in the posterior margin of their lateral line scales (Nelson 1986). However, at the focus of their scales where posterior limit of canal roof and anterior end of notch converge, a small pore is observed beneath the roof. The pore diameter is less than width of canal roof. Thus, the plesiomorphic

lateral line scale pore morphology has a more centrally located canal pore with diameter less than width of canal.

Two additional states describe lateral line morphology. State (1) represents posteriorly displaced lateral line canal pore on the scales posterior margin with diameter approximately equal to width of canal. State (2), illustrated by *Gymnamodytes* (Fig. 107) describes a scaleless lateral line constructed of an alternating system of horizontal tubules and vertical tubules.

Character 28: Dorsal triangular process on the interoperculum (Fig. 112, **IOPP**). A small dorsal triangular process is present on the interoperculum of all ammodytids, trichonotids (Figs. 111-113) and most uranoscopids (Pietsch 198, fig. 26). It acts as an attachment site for ligaments that originate from distal epihyal.

Character 29: Extrascapulars large and well ossified. (Fig. 119, **ES**). This character was described in Pietsch and Zebatian's (1990) study. However, contrary to Pietsch and Zebatian's observation, trichonotids possess well ossified, large extrascapulars (Fig. 120) as well.

Character 30: One extrascapular or two with evidence of fusion (Fig. 119, **ES**). Pietsch and Zebatian (1990, fig. 2) illustrated *E. mitsukurii* with three extrascapulars and trachinids or uranoscopids have three or more (Pietsch, 1989, fig. 8, 15). Trichonotids have two (Fig. 120) and species of *Hyperoplus*, *Gymnamodytes* and *Ammodytes* possess

one. Smaller individuals of *Ammodytes americanus* show two elements apparently in the process of fusing (Fig. 119) because there is some union on the medial side and larger specimens of *Ammodytes* always have one extrascapular. Primitively, the number of extrascapulars are therefore two or more. The derived state has one extrascapular although there may be two with evidence of fusion on smaller individuals.

Character 31: Medial extrascapular not fused to posterior cranium (Fig. 119). This character follows Pietsch and Zebatian (1990) who found that fusion of medial extrascapular to posteromedial supraoccipital occurs in trachinids and uranoscopids. Such an observation is consistent with the posterior positioning of extrascapular elements in these fishes (Pietsch 1989, fig. 8, 15). Fusion is also observed in Trichonotidae (Fig. 120) but it occurs with the parietals and corresponds with an anterior shift of extrascapulars. A similar shift is also observed in ammodytids but their extrascapulars are free (Fig. 119, Pietsch and Zebatian 1990, fig. 2). These shifts may be related to elongation of anterior-posterior cranial axis and abbreviation of cranial width. Consequently, fusion is reinterpreted to mean fusion to any bones of posterior cranium. Fusion occurs invariably in the outgroup (Trichonotidae, Uranoscopidae and Trachinidae) and is thus considered plesiomorphic, despite the fact that it was

apomorphic in Pietsch and Zebatian's (1990) more inclusive trachinoid study. Free extrascapulars are assumed to be derived.

Character 32: Hyohyoidei adductores muscle with anterodorsal section greatly restricted (Figs. 121, HYO-AD). Greatly restricted anterodorsal section of hyohyoidei adductores muscle was one of eight character used by Pietsch and Zebatian (1990) to support Uranoscopidae, Trachinidae, Ammodytidae monophyly (Fig. 121). Unfortunately, they overlooked its presence in trichonotids (*Trichonotops*, Fig. 122). Many perciforms (*Morone*, *Chichlasoma*) and trachinoids (*Cheimarrichthys*, *Leptoscopus*) exhibit a broad sheet of muscle over the medial side of their operculars and this condition has been regarded as plesiomorphic (Pietsch 1989, Pietsch and Zebatian 1990).

Character 33: Lateral line elevated and turning ventrally on caudal peduncle (Jordan and Evermann, 1902, fig. 12, Fowler, 1931, fig. 13). Lateral line elevated and turning ventrally on caudal peduncle was another character corroborating monophyly of ammodytids, uranoscopids and trachinids (Pietsch and Zebatian, 1990). Webb (1989b) used Uranoscopidae as an example and briefly mentioned that dorsal displacement of the lateral line trunk canal was found in many benthic 'sit and wait' predators (Webb, 1989b, p. 47) but did not discuss phylogenetic implications of this character state. More comprehensive studies are thus

necessary to assess the distribution of dorsally displaced lateral lines but lack of substantial data showing that dorsal displacement is more widely found among percomorphs and strong support of the uranoscopid, trachinid and ammodytid node with other character, justifies its utilization in this analysis. Trichonotids lack this condition, displaying a mid-flank lateral line which does not deviate as it nears the caudal peduncle. Such lateral line morphology is assumed to be plesiomorphic (Pietsch and Zebatian 1990).

Character 34: Sphenotic with posteroventrally directed process (Kayser 1961, fig. 2-4, Pietsch and Zebatian 1990, figs. 2-4). Occurrence of a postero-ventrally directed process on the sphenotic in ammodytids and trachinids was noted and well documented by Kayser (1961), Pietsch (1989) and Pietsch and Zebatian (1990).

Character 35: Epiotic with small triangular shelf of bone over which lies the dorsal arm of the posttemporal (Fig. 119, EPOS). Homology of posterolateral expansion of epiotics in trachinids with those of uranoscopids (Pietsch 1989, fig. 10 and ammodytids (Pietsch and Zebatian 1990, fig. 2, Fig. 119) seems doubtful given the exaggerated structure exhibited by *Trachinus* (Pietsch 1989, fig. 8). *Trachinus* displays more similarity with other groups of perciforms such as pleuronectiforms (Chapleau 1993, fig. 4) and labrids (Westneat 1993, figs. 5-8). Compared to

trachinids, the small shelf jutting from epiotics which supports the dorsal arm of posttemporal (Fig. 119, **EPOS**) in ammodytids and uranoscopids is more accurately termed, *reduced epiotic expansion*. A highly reduced shelf has also been observed in trichonotids (Fig. 120). Hence, large epiotic expansions on trachinids is typical of the primitive state and triangular reduced processes of ammodytids, uranoscopids and trichonotids are derived.

Character 36: Cutaneous axillary appendage associated with pectoral fin (Pietsch and Zebatian 1990, fig. 20). Homology of cutaneous axillary appendages in Ammodytidae, Trachinidae and Uranoscopidae is difficult to disprove but questions invariably arise concerning their homology because these families have not been carefully scrutinized osteologically (Johnson 1993). For example, comparison of gill arches from uranoscopids and ammodytids (Rosen and Patterson 1990, fig. 36, Figs. 130-137) reveals little resemblance. Nevertheless, homology of the axillary appendages is hard to refute as it seems to occur only in these three families and remains one of the principal synapomorphies justifying ammodytid, trachinid and uranoscopid monophyly (Pietsch and Zebatian 1990).

Character 37: Supracleithrum superficial, surface rugose and highly sculptured (Pietsch 1989, fig. 10). In Pietsch and Zebatian's (1990) analysis this character was used to support a monophyletic Trachinidae, Uranoscopidae

clade. It is utilized in this analysis because of its relevance to outgroup relationships which can influence ingroup phylogeny (Maddison et al. 1984). Supracleithrum covered by thick skin is the alternative state observed in ammodytids, remainder of trachinoids (Pietsch and Zebatian 1990) and many acanthomorphs.

Character 38: Caudal peduncle supported by five or more blade-like neural and haemal spines (Fig. 127, NPU3, HPU3). Gosline (1963) used blade-like neural and haemal spines as one of his defining character for Ammodytidae. Nonetheless, *Embolichthys* and *Bleekeria* (Fig. 17a, Pietsch and Zebatian 1990, fig. 15, Ida 1976, fig. 6) do not exactly exhibit this morphology. Instead, they have long, slender spines which come to relatively blunt points. All other genera of ammodytids, typified by *Ammodytes hexapterus* (Fig. 127) and *Gymnammodytes capensis* (Fig. 17b), display a more obviously shortened blade-like condition which Gosline (1963) apparently described. Comparison of blade-like spines (Figs. 126, 127) to those from *Embolichthys* (Fig. 17a), *Trichonotops* (Fig. 128) or *Uranoscopus* (Pietsch 1989, fig. 32) indicate that the blade-like condition is unique because no caudal peduncular neural (Fig. 127, NPU3) or haemal spines (HPU3) are long and narrow. However, *Uranoscopus* does show broad NPU3 and NPU4, but the blade-like condition on both haemal and neural spines is unique to *Ammodytes*, *Gymnammodytes* and *Hyperoplus*. Consequently, the elongate

neural and haemal spines of *Embolichthys* (Pietsch and Zebatian 1990, fig. 15) are judged primitive and the bladeliike spines of *Ammodytes* (Fig. 127) are derived.

Character 39: Small shelf of bone jutting anteriorly from operculum which receives elongate anterodorsal process of suboperculum (Fig. 113, OPS). The elongate anterodorsal arm of suboperculum fits laterally over or into the ventral notch of a small, anteriorly projecting shelf of operculum. The shelf forms approximately one third upper anterior opercular margin below posterior arm of hyomandibula (Figs. 112, 113, OPS). The character provides further evidence of Ammodytidae monophyly since it is unique to this family. Absence of the shelf is interesting in trichonotids because they preserve an elongate anterodorsal subopercular process.

Character 40: Supraoccipital relatively flat with elongate anterior process and posterior wings of laminar bone (Fig. 115). Primitively, percomorph supraoccipitals have prominent posterior crests and the bone falls off sharply on either side of crest before it joins exoccipitals posteroventrally (Pietsch 1989, fig 14). Example of this osteology can also be viewed in Gregory (1933, figs. 118-130). Flattened supraoccipitals lacking a prominent crest are observed on some zoarcoids (Gregory 1933, fig. 254), blennioids (Gregory 1933, figs. 251, 254), ammodytids and trichonotids (Figs. 115).

Anterior processes of supraoccipitals are difficult to

observe without completely disarticulating skull because frontals usually overlap them (Gregory 1933, fig. 234, Figs. 119, 120). Gregory pictured anterior processes on isolated supraoccipitals from *Clinus*, *Zoarces* and *Lates niloticus* (1933, figs. 118, 254) but they are not commonly displayed features of supraoccipital osteology. Examination of a large skeletonized specimen of *Morone saxatilis*, by looking posteriorly into brain cavity from the orbit, revealed a short and wide anterior supraoccipital process underneath the frontals.

Prominent crests and shortened anterior processes are frequently linked, although there are exceptions. For example, *Lates* (Gregory 1933, fig. 118), which has an obvious crest, was pictured with a prolonged anterior process. Flattened supraoccipitals with reduced crests and more elongate anterior processes are also associated osteological features of the supraoccipitals but occurrences in phylogenetically unrelated groups (*Clinus*, *Zoarces*, *Ammodytes*) suggests that they may have arisen independently a number of times. The common factor in fishes with reduced crest and flattened supraoccipital is skull elongation but a more detailed survey of supraoccipital osteology is needed to confirm this trend.

The primitive supraoccipital is epitomized in the outgroup by uranoscopids and trachinids who possess short, wide anterior processes, prominent crests and postero-

ventral deflections of bone on either side of crest as it meets exoccipitals (Rosen 1985, figs. 28-30, 32, Pietsch 1989, figs 8, 11). The derived state is assumed to occur in ammodytids and trichonotids. They exhibit flattened supraoccipitals, greatly reduced crests, elongate anterior processes, posterolateral extensions of laminar bone and short square posterior extensions (Fig. 115).

Character 41: Entire length of dorsal fin in a deep groove. Ammodytidae, Trachinidae and Uranoscopidae have entire length of their dorsal fins in a deep groove (Pietsch and Zebatian 1990) and use of this character as a synapomorphy further bolstered the case for their monophyly. However, fundamental differences between the dorsal fin anatomy of ammodytids (continuous fin, no fin spines, predorsal bones present only in *Embolichthys* and easily distinguished from ray bearing pterygiophores, Pietsch and Zebatian 1990, fig. 14), uranoscopids (spinous dorsal fin, except for *Ichthyscopus* and *Astroscopus*, predorsals present and proximal pterygiophores deeply set between neural spines, morphology of predorsal indistinguishable from spine or ray bearing pterygiophores, Pietsch 1989, fig. 30) and trachinids (spinous dorsal fin) provides circumstantial evidence that says the grooves are homoplasious. On the other hand, similarities (Pietsch and Zebatian 1990) in dorsal fin morphology between ammodytids, uranoscopids and trachinids (approximate one to one relationship of dorsal

pterygiophore to neural spines) or trachinids and ammodytids (only proximal tip of pterygiophores lie between neural spines) lends ancillary support for homology of their grooves. At the moment, lack of any direct evidence refuting their homology makes occurrence of groove a compelling synapomorphy. Absence of a dorsal fin groove is assumed to be primitive since this state was confirmed in all acanthomorphs, percomorphs, perciforms and other trachinoids examined.

Character 42: Scales not in tight chevrons on ventral surface (Reay 1986, figs. 6, 7, p. 946). On ventral surface or belly of *Ammodytes tobianus* scales generally overlap or are in tight chevrons. Scales in tight chevrons are assumed to be plesiomorphic as they widely occur in acanthomorphs, outgroup and putatively more primitive ammodytids *Embolichthys* and *Bleekeria*. Widely spaced placement of scales is considered derived and observed on ventral body surfaces of *Ammodytes*, (except *A. tobianus*), *Hyperoplus* and *Gymnammodytes*.

Character 43: Absence of scales up to and just anterior to dorsal fin (Reay 1970, 1986). Reay (1970, 1986) found *Ammodytes marinus* lacks scales just anterior to and along side dorsal fin while *A. tobianus* has them directly abutting the fin. Occurrences of scales directly adjoining anterior dorsal fin in outgroup, most acanthomorphs, *Embolichthys* and *Bleekeria* is evidence of its plesiomorphy. Whereas the

scaleless gap observed on all other species of *Ammodytes*, *Hyperoplus* and *Gymnammodytes* is derived.

Character 44: Last dorsal pterygiophore simple and bearing only one ray. Robins and Böhkle (1970) noted that *E. mitsukurii*, *E. sarisa* and *B. viridianguilla* have two serial rays on the ultimate pterygiophore, the last split to its base. This feature is observed in uranoscopids and trichonotids (Nelson 1986, fig. 3, Fig. 128), although Nelson (1986) wrongly pictured the last ray fused at its base. Trachinids apparently have two side by side rays on last pterygiophore. Since two rays positioned serially on last pterygiophore predominate in the outgroup, it is considered plesiomorphic. Articulation of two rays on last dorsal pterygiophore also has a wide distribution in other groups and is further evidence that the state is plesiomorphic. For example, Gill and Hoese (1993, fig. 10) pictured a two ray serial morphology for the new gobioid genus and species *Paraxenisthmus springeri* and Gill and Mooi (1993, fig. 13) for *Notograptus*. The derived condition is typified by *Ammodytes* which has a 'simple' ray on the last pterygiophore (Robins and Böhkle 1970) and the ray is also cleft to its base.

Character 45: Loss of teeth on the premaxillary and dentary (Fig. 110). Presence of teeth on premaxillary and dentary of ammodytids was discussed by Robins and Böhkle (1970) when they described *E. sarisa*. They noted that

Embolichthys mitsukurii (see also Pietsch and Zebatian 1990, fig. 9) and *Bleekeria viridianguilla* have premaxillary-dentary teeth while *E. sarisa* (Robins and Böhkle 1970), *B. renniei* (Smith 1957) and *B. gilli* (Gosline 1963) lack them. Widespread occurrence of premaxillary and dentary teeth in acanthomorphs and outgroup demonstrate presence of teeth is plesiomorphic whereas loss of teeth observed in most ammodytids is considered derived.

Phylogenetic Analysis

Decisions concerning ordering multi-state characters resulted from an iterative process of testing character state optimizations on strict consensus trees generated by a combination of unordered characters and hypothetical transformation series ordered by either examining optimizations on preliminary trees or application of Lipscomb's (1992) similarity criterion. Reanalysis was continued until a satisfactory most parsimonious consensus tree is derived which balances unordered characters with character state optimizations influenced by a particular transformation series hypotheses, length of most parsimonious trees and greatest resolution.

Characters 2, 5, 8, and 19 are run nonadditively or unordered because their optimizations on preliminary consensus cladograms (Fig. 138) and the final proposed cladogram (Fig. 139) of Ammodytidae interrelationships obscured any clear phylogenetic succession of states. Ontogenetic transformations from a two field scale to either a membranous ctenoid scale or transformed ctenoid scale was shown by Lui and Shen (1990) but the scale type that precedes either adult ammodytid types (Character 2) is unknown. The smallest specimen of *Ammodytes* (62 mm long) which yielded scales showed the characteristic ammodytid morphology, although rudimentary. Thus, no ontogenetic

evidence is available to suggest a transformation series that led to an ammodytid scale with posterior radial ridges. Occurrence of two field scales in Uranoscopidae and Trachinidae (Figs. 9, 10) of outgroup implies that ammodytid scales could have arisen from a two field ancestor, except that another outgroup taxon, trichonotids, have scales similar to those from ammodytids. Consequently, scales of trachinids and uranoscopids could be examples of developmental truncation or reversal while ammodytid and trichonotid scales reflect the typical four field scales of percomorphs with greater than five anterior field scalelets.

Scale shapes do not appear to adhere to any ordered patterns of transformation (Character 5) with their mosaic distribution across various taxa and clades. Plesiomorphic pentagonal scales are characteristic of *Embolichthys mitsukurii*, *Bleekeria viridianguilla* and *Trichonotops*. Round scales occur in trachinids, *Bleekeria renniei*, *Hyperoplus* and *Gymnamodytes*. Fragile elliptical scales are found in *Bleekeria gilli*, *Ammodytes tobianus*, *A. americanus* and *A. dubius* whereas more angular stout scales are distinctive to *A. personatus*, *A. hexapterus* and *A. marinus*.

Elongate terminal lateral line caudal scales (character 8) with a tubular canal occurs in Leptoscopidae and one member of the outgroup, Trichonotidae. The ultimate caudal lateral line scale with an open perforated groove then appears in *Ammodytes*, *Hyperoplus* and *Gymnamodytes*.

Consequently, ambiguity in terms of distribution of taxa with elongate lateral line caudal scales negates any clear conclusions concerning their transformations. In addition, the tubular canal on the ultimate lateral line caudal fin scale of leptoscopids and trichonotids suggests they may not be homologous with the perforated grooved scales of ammodytids. Dorsal body pigmentation of larvae (character 19) extending to tip of notochord occurs mosaically in *E. mitsukurii*, *B. viridianguilla*, *A. dubius*, *A. marinus* and *A. hexapterus*. Therefore, it is uncertain whether this state arose from a dorsally pigmented intermediate or the primitive unpigmented condition.

Ordering of characters 6, 7, 13, 14, 15 and 27 are based upon the following evidence and arguments. Appearance and disappearance of lepidonts (character 6) do not have any particular noteworthy phylogenetic pattern because of a mosaic distribution in the outgroup. Scales from trachinids and uranoscopids lacked lepidonts but trichonotids (Fig. 93) have them. However, a generalized pattern occurred in ammodytids where the more derived *Ammodytes*, *Hyperoplus* and *Gymnammodytes* (Figs. 138-140) did not exhibit lepidonts (Figs. 88-91) while the more plesiomorphic *Embolichthys* and *Bleekeria* display them (Figs. 83-87), albeit greatly reduced or absent in some species of *Bleekeria* (Fig. 87).

Initially, Character 7 was ordered so that character states of scale field symmetry followed their distribution

in taxa on Figure 138. Thus, scales with high field symmetry transform into scales with highly distorted field symmetry and then to scales with moderately distorted field symmetry. This hypothesis causes the *Bleekeria gilli* - *B. renniei* node to collapse (Fig. 138). However, the transformation of high field symmetry ---> moderate field asymmetry ----> high field asymmetry is chosen over the first hypothesis because it produces better resolution with a monophyletic *B. renniei* and *B. gilli* (Tab. 4, Fig. 139). Placement of *B. renniei* and *B. gilli* in a separate clade is supported by additional lepidological and labial ossicle evidence which could ultimately lead to their location, along with *Bleekeria vaga* and new species *Ammodytoides kimurai*, in genus *Ammodytoides* (Figs. 71, 72, 80-82, Duncker and Mohr 1939, Ida and Randall 1993). The ordering sequence of scale symmetry is also justified in terms of parsimony and adjacency principle (Lipscomb 1992) because it minimizes the amount of change neighboring states exhibit. Therefore, a transformation hypothesis correlating with increased levels of scale field distortion gives better resolution (fig. 139). *Embolichthys* has the least amount of field distortion, *Ammodytes*, *Hyperoplus* and *Gymnammodytes* show moderate distortion and *Bleekeria* the most.

The cladograms of figures. 138 and 139 suggest that body scale patterns (Character 13) apparently follow this sequence: overlapping scale -----> scales in oblique rows -

-----> scales absent over most of body flanks except caudal peduncle. Oblique scale rows are homoplastically distributed in trachinids - uranoscopids and *Ammodytes* - *Hyperoplus* while *Gymnammodytes* are nearly naked. Occurrence of oblique scale rows in trachinids and uranoscopids is difficult to evaluate but parsimoniously appears to be an independent derivation since it would have to be a reversal all in basal ammodytids if its incidence in *Ammodytes* and *Hyperoplus* is viewed as synapomorphic with trachinids and uranoscopids. Trichonotids have the plesiomorphic condition of overlapping scales as does *Embolichthys* and *Bleekeria*. Consequently, scales in oblique rows and loss of scales could have arisen from a common overlapping scaled ancestor but optimization of states on the consensus tree (Fig. 13) suggests otherwise.

Character (14) is ordered because its optimization on the cladograms (Figs. 138, 139) implies that truncated ventrolateral skin folds of *G. capensis* and *G. semisquamatus*, arose from the more common extended skin folds observed in *Ammodytes*, *Hyperoplus* and *G. cicereus*. Prolonged skin folds are thus derived from ancestors without folds since *Embolichthys*, *Bleekeria* and all outgroup taxa lack folds.

Morphology of the lateral line scale and pore system (Character 27) appears to follow this transformation series: small pore canal pore positioned well anterior from

posterior scale margin -----> large pore, positioned on the anterior scale margin -----> scaleless lateral line with system of vertical and horizontal tubules ending in pores. Cladograms of figures 138, 139 urge acceptance of the sequence because the primitive condition of small pored lateral line scales are found in the outgroup, plesiomorphic ammodytids (*Bleekeria* and *Embolichthys*) and is common among perciforms. Large pores on the posterior margin are found only in *Ammodytes* and *Hyperoplus*. The most derived condition of scaleless lateral line with alternating vertical and horizontal tubules is a specialization unique to *Gymnammodytes*.

Before ordering character (15) (extra labial cartilages and ossicles) five transformation series hypotheses were tested. There are five states and they are initially based upon the following numbering system:

- (0) - No extra labial ossicles or ligaments.
- (1) - Presences of labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, premaxillo-rostral cartilages and ligaments and cartilages IV and V.
- (2) - Ossicles replacing cartilages of state (1).
- (3) - Possession of following ossicles: labial 6 and 2, maxillo-dentary, maxillo-vomerine, fused maxillo-premaxillary and lateral maxillo-premaxillary; premaxillo-rostral ligament absent, accessory labial cartilages absent.
- (4) - Same ligaments and cartilages as state (1) except premaxillo-rostral ligament and accessory labial cartilages absent.

The transformation series hypotheses are given below:

Hypothesis (1)

0 -----> 1 -----> 2 -----> 3 -----> 4

Hypothesis (2)

0 -----> 1 -----> 2 -----> 4 -----> 3

Hypothesis (3)

0 -----> 1 -----> 4 -----> 3 -----> 2

Hypothesis (4)

0 -----> 1 -----> 2
 |-----> 3
 |-----> 4

Hypothesis (5)

0 -----> 1 -----> 3 -----> 2
 |-----> 4

Hypothesis (1) (Fig. 138) correlated with the phylogenetic position of genera that possessed the state on tentative test trees (Figs 1b, 138). Hypothesis (1) has loss of ossification when state (2) transforms to (3) arising simultaneous with loss of premaxillo-rostral ligament and accessory labial cartilages. Hypothesis (2) emphasizes loss of premaxillo-rostral ligament and accessory labial cartilages as state (4) succeeds state (2), whereas ossification arose independently in states (2) and (3). Application of Lipscomb's (1992) similarity criterion places the most homologous states adjacent to each other in the transformation series and serves as the basis of

hypothesis (3). Ossifications of cartilages to a single event is postulated when state (4) transposes to state (3). Partial ossification of some cartilages in state (3) converts to full ossification of all cartilages in state (2). Hypotheses (1), (2) and (3) were tested by simply reordering character (15) (Tab. 4). For example, in hypothesis (3) states (1) remains exactly the same whereas state (4) became state (2) and state (2) is the ultimate state.

To accommodate branch points of hypotheses (4) or (5), character (15) was modified into a three character complex. For hypothesis (4) two new characters, (16) and (17) are made autapomorphies for cartilage (state 4) or ossicle morphology (state 3) observed in *Ammodytes* and *Gymnammodytes*, respectively (Tab. 5). Hypothesis (5) (Tab. 6) was also accommodated by contriving two new characters, (16) and (17). State (1) (full set of ligaments and cartilages) gives rise to either state (4) (character 16) (loss of accessory labial cartilages and premaxillo-rostral ligament) or sequence of character (17) where state (3) (loss of accessory labial cartilages and premaxillo-rostral ligament with ossification and fusion of some cartilages) transforms to ossified cartilages of state (2).

Hypotheses were tested by comparing most parsimonious trees and consensus tree statistics which relate to a particular hypothesis (Tab. 8). The shortest trees came

from hypothesis (2). A strict consensus tree is illustrated in Figure 139. Application of Lipscomb's (1992) similarity criteria may be useful in some cases but limiting one to preconceived notions of similarity can obscure patterns of homology in other characters states. For example, degree of ossification of labial cartilages was the similarity criteria of hypothesis (3) but a data set accommodating hypothesis (2) generated more parsimonious trees (Tab. 8). This hypothesis revealed that loss of accessory cartilages and premaxillo-rostral ligament could be more significant phylogenetically than degree of ossification. Therefore, an ammodytid with a full set of ligaments and cartilages (state 1) transforms into one with cartilages fully ossified (state 2), followed by total reversal of ossification and loss of accessory labial cartilages and premaxillo-rostral ligaments and finally reossification of two labial cartilages (II & VI), maxillo-vomerine cartilage and maxillo-premaxillary cartilage which fuses with ossicle formed from lateral maxillo-premaxillary cartilage.

Three taxon transformations for phylogenetic analysis has not gained widespread acceptance in the systematic literature (Harvey 1992, Kluge 1993). It is a novel hypothesis which has been virtually untested (Platnick 1993) but curiosity, attractive theoretical possibilities in terms of reduction of phylogenetic character data to their most basic informative unit (Platnick *et al.* 1991, Nelson and

Platnick 1991) and potential for minimizing spurious effects due to missing data (Nelson and Ladiges 1993), led to utilization of three taxon analysis in this work. A three taxon statement transformation matrix generated by TAX was obtained using the data matrix of hypothesis (2). With fractional weighing, 1736 unique characters were derived. Three parsimonious tree were calculated using PAUP's heuristic tree search algorithm and the random stepwise addition option. The consensus tree is shown in Figure 140 and with data set of hypothesis (2) (Tab. 4) optimized on Figure 140 the tree had a length of 78, ci = 73, ri = 87. Nevertheless, these results are not radically different than those found by straight parsimony analysis (Figs. 2a, 139) except Figure 140 shows a sister group relationship between *Ammodytes* and *Hyperoplus* apparently based upon the common possession of plicae.

The three taxon transformation consensus tree (Fig. 140) and conventional parsimony tree (Fig. 139) actually reinforce one notion of ammodytid relationships although it calls for additional supporting data. Ida (work in progress) postulated *E. sarisa* was the most plesiomorphic ammodytid because it has the most well developed pelvic fins. Occurrence of concentric ridges in its posterior scale field is a primitive lepidology which further strengthen Ida's hypothesis. It was thought possession of membranous cteni in mugilids could help polarize this state

in *E. sarisa* but membranous cteni could also be an independent derivation since there is no other evidence that mugilids and ammodytids are related (see pg. 218).

Succeeding discussions pertain to the most parsimonious consensus tree (Fig. 139) generated by raw data (Tab. 4) under influence of hypothesis (2). Synapomorphies suggesting a relationship of Ammodytidae, Trachinidae and Uranoscopidae include:

1. Lateral line elevated and turning ventrally on caudal peduncle.
2. Cutaneous axillary appendage over pectoral fin.
3. Sphenotic with a lateral posteroventrally directed process but lost in uranoscopids.
4. Entire length of dorsal fin in a deep groove.

Closer relationship of trichonotids to ammodytids is supported by homologies in posterior scale field morphology (Compare Figs. 13, 97 to 70, 96), elongate dorsally directed subopercular process (Fig. 112-114) and supraoccipitals osteology with flat profile, reduced crest, elongate anterior process and posterolateral wings of laminar bone (Fig. 115). Trichonotids superficially resemble ammodytids with their eel-like shape, lack of spiny fin rays, and burrowing behavior (Smith 1936, Clark and Schmidt 1966, Kotthaus 1977, Shimada and Yoshino 1984, Nelson 1986) and larval morphology (Leis and Rennis 1984, Leis and Trnski 1989). However, other characters shared between trichonotids - uranoscopids - ammodytids (small triangular

shelf on their epiotics, Figs. 119, 120, Pietsch 1989, fig. 10, dorsally directed process on interoperculars, Figs. 112-114, Pietsch 1989, fig. 26), trachinids - uranoscopids - trichonotids (medial extrascapular fused to the cranium) or trichonotids - uranoscopids - trachinids - ammodytids (restricted hyohyoideus muscle, Figs. 121, 122, well ossified extrascapulars, Figs. 119, 120) and uranoscopids - trachinids - ammodytids, cause ammodytids, trichonotids and trachinids plus uranoscopids to assume a polytomous relationship (Fig. 139). Relationships of Trachinidae, Uranoscopidae and Ammodytidae (Pietsch and Zebatian 1990) survived one round of testing but Trichonotidae appear linked to these families as well. There is undoubtedly some synapomorphic support for a uranoscopid - trachinid - ammodytid relationship, although wide differences in basic osteological features, such as gill arches and caudal skeleton reveal the weaknesses of this hypothesis.

Monophyly of Ammodytidae is supported by the following specializations. The first four come from Pietsch and Zebatian (1990).

1. Complex arrangement of extra cartilages and ossicles in jaw.
2. Anteriorly directed symphyseal process on dentary.
3. Large oval foramen in dentary.
4. Anterodorsally directed spine-like process on lateral surface of metapterygoid.
5. Anteriorly projecting shelf of bone on

upper anterior margin of operculum which receives dorsal tip of an elongate anterodorsal subopercular process.

Symplesiomorphies which set *Embolichthys* and *Bleekeria viridianguilla* apart from rest of ammodytids are overlapping scales, pentagonally shaped scales with anterior field scalelets separated by sulci, scale fields symmetric or almost, pungent lepidonts on scales anterior ridges, pharyngobranchial in serial arrangement (per interpretation of Rosen 1973) and two serial rays on ultimate dorsal pterygiophore cleft to their bases. Monophyly of *Embolichthys sarisa*, *Bleekeria* (minus *B. viridianguilla*, *Hyperoplus*, *Gymnammodytes* and *Ammodytes* is justified by only one character, absence of teeth on premaxillary and dentary.

Monophyly of *Bleekeria* (minus *B. viridianguilla*), *Gymnammodytes*, *Hyperoplus* and *Ammodytes* is supported by the following shared derived characters:

1. Modification of lateral line scales with either pore near or at posterior scale margin or scaleless lateral line constructed of alternating vertical and horizontal tubules.
2. Round or elliptical scales.
3. Distortion of scale field symmetry
4. Ossification of some or all labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, premaxillo-rostral, IV and V cartilages and or loss of premaxillo-rostral ligament and accessory labial cartilages.
5. Single ray on ultimate dorsal pterygiophore.

A monophyletic clade comprised of *Gymnammodytes*, *Hyperoplus* and *Ammodytes* is well substantiated by these synapomorphies:

1. Anterior field scalelets separated by relatively wide radial ridges, not sulci.
2. Concentric ridge around nucleus perforated by anterior radial ridges.
3. Ventrolateral skin folds.
4. Nasal organ smooth and oval.
5. One extrascapular but there may be evidence of fusion with additional extrascapular elements on smaller specimens.
6. Neural and hemal spines of caudal peduncle are blade-like and wide.
7. Lateral line terminates over middle of hypural plate with an elongate, spade shaped scale, bisected longitudinally by perforated groove.

Hyperoplus, *Gymnammodytes* and *Ammodytes* minus *A. tobianus* are related by sharing absence of scales on caudal fin musculature, widely dispersed scales on ventral body surface and absence of scales just anterior to and along side dorsal fin. Homoplasy is also common in this clade but they appear to be independent derivations in outgroup or other taxa. Oblique scales rows occur in *Ammodytes* - *Hyperoplus* as well as Trachinidae - Uranoscopidae. Absence of larval ventral fin membrane pigment is found in Uranoscopidae and *Hyperoplus* - *Ammodytes*. Monophyly of the *Hyperoplus* - *Gymnammodytes* is supported by only one dubious synapomorphy, round scales, which also occurs

homoplastically in Trachinidae and *B. renniei*. Figure 139 suggests that the larval vomerine fangs of *Hyperoplus - Gymnammodytes* may be homologous.

Relationship of *Embolichthys* and *B. viridianguilla* are principally supported by a synapomorphy complex of these labial cartilages and accompanying ligaments: labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, premaxillo-rostral and cartilages IV, V. They also share great similarity in posterior scale field morphology with well defined radial ridges and blunt spines on posterior margin (Figs. 70, 96). The only obvious difference between *Bleekeria viridianguilla* and *Embolichthys mitsukurii* is possession of pelvics in the latter. One *E. mitsukurii* of lot USNM 59599 lacked pelvics and examination of more individuals of *E. mitsukurii* might show it is polymorphic with regard to possession of pelvic fins. Loss of pelvic girdle in some individuals could be perceived as full manifestation of a degenerative mechanism exhibited in the rudimentary pelvics of *Embolichthys*. Therefore, it would not be surprising if *Bleekeria viridianguilla* is simply *Embolichthys mitsukurii* without pelvic fins. In fact, except for absence of pelvic fins it is extremely difficult to distinguish the two. There is one subtle difference pertaining to more widely spaced anterior scalelet ridges in *B. viridianguilla* (Figs. 12, 70) but this could be due to environmental variability in specimens

sampled. *Embolichthys mitsukurii* and *Bleekeria viridianguilla* also share the following similarities: dorsal and anal ray counts, head length, body depth, eye size, snout length, same number and kinds of labial ligaments (Ida 1973) and larval pigmentation patterns (Leis and Trnski 1989). In any case, *B. viridianguilla* probably does not belong in *Bleekeria* because its scales and labial cartilages suggest a closer relationship to *E. mitsukurii*.

The genus *Bleekeria* (minus *B. viridianguilla*) is defined by the possession of labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, and premaxillo-rostral ossicles. It is also characterized by scales with greatly distorted field symmetry where ventral lateral field overlaps the posterior field forming part of posterior margin. *Bleekeria renniei* and *B. gilli* also have reduced dull lepidonts on ridges of the anterior field scalelets.

Synapomorphies shared by all species of *Gymnamodytes* include:

1. Anterior half of body practically naked, posterior half has widely dispersed scales.
2. Scaleless lateral line constructed of horizontal and vertical tubules. One pore in between every horizontal tubule and another pore at dorsal end of vertical tubules which arises in between every other horizontal tubule.
3. Labial 2 and 6, maxillo-dentary, maxillo-vomerine and fused maxillo-premaxillary and lateral maxillo-premaxillary ossicles.

Gymnammodytes capensis and *G. semisquamatus* are more closely related to each based upon specialization of ventrolateral skin fold ending just past tip of pectoral fin. The plesiomorphic state, observed in *G. cicereus*, *Hyperoplus* and *Ammodytes*, finds the skin fold terminating just past anterior margin of anal fin.

Monophyly of *Hyperoplus* is substantiated with two synapomorphies.

1. Two large fangs on vomer and anterior tip of the vomer is notched (Einarsson 1951, figs. 6, 7).
2. Medial maxillary process wide with a medial projection on base of maxillary cranial process (Fig. 108)

A monophyletic *Ammodytes* is not supported by data. *Ammodytes tobianus* has a number of plesiomorphic characters which cause it to assume a more primitive position relative to remainder of species in genus. These include: scales on the caudal fin musculature, scales anterior to dorsal fin and scales in tight chevrons on ventral surface; lack of ventral body pigment on larvae and absence of caudal pigment in small larvae less than 15 mm long.

Two subgroups within the residue of *Ammodytes* are discernable. *Ammodytes americanus* and *A. dubius* share a narrower terminal caudal lateral line scale (Figs. 98, 99) than *Ammodytes marinus*, *A. hexapterus* and *A. personatus* (Figs. 100). The latter three species share similarities in scale morphology (Figs. 73-75). Their scale are more robust

and ossified with clearer field definition and angularity than those of *A. americanus* or *A. dubius* which have more elliptical scales (Figs. 77-78). A fully resolved unambiguous phylogeny of *Ammodytes* remains an elusive goal.

Patterns of lepidological variation parallels the morphological vicissitude of labial cartilages, ligaments and ossicles. The two genera with maximal differences in labial cartilages and scale morphology are adjacent on the cladograms (Figs. 2b, 138-140). *Embolichthys* has full set of labial cartilages and pentagonal symmetric four field scales while *Bleekeria* shows ossification of same cartilages and round or elliptical scales with highly distorted field symmetry. An analogous degree of difference between their scales and labial cartilages, ligament and ossicles are observed between the genera *Gymnammodytes* - *Hyperoplus* - *Ammodytes*. They all share loss of accessory labial cartilages and premaxillary-rostral ligament and moderate field asymmetry. *Gymnammodytes* displays the greatest dissimilarity in regard to labial ossicles and scale morphology compared to the other two taxa by having ossified labial cartilages and extremely fragile, highly reduced scales. Therefore, it appears that there is similarity relating to degree and patterns of variability between ammodytid genera in two widely distinct morphological systems and this is strong evidence that such patterns are due to the same phylogenetic process. However, while the

Ammodytes, *Hyperoplus* and *Gymnammodytes* clade is strongly supported by synapomorphy, the generic and specific relationships (Fig 139) within this clade and especially *Ammodytes* are obscure due to deficiency of synapomorphies relevant to hierarchical ordering of their relationships (Fig 139).

Discussion

Relationship of Ammodytidae to Perciformes

Ammodytidae have usually been considered an offshoot of Perciformes (Gosline 1968, Nelson 1984, Pietsch and Zebatian 1990) and placed in their own suborder, Ammodytoidei (Greenwood *et al.* 1966, Lauder and Liem 1983) or superfamily Ammodytoidea (Gosline 1968). Gregory (1933) thought they might be percomorphs but could find no "...hint of derivation." (p. 354) and had them *incertae sedis*. Gosline (1963) compared ammodytids to elongate perciform fishes, *Parapercis schauinslandi* (Parapercidae), *Crystallodytes cookei* (Creedidae) and *Trypterygion atriceps* (Tripterygiidae). He drew no conclusion on relationships when he stated: "The majority of features point to a percoid origin of some sort but none of the percoid families known to the author would seem to provide a suitable ancestor" (Gosline 1963, p. 80).

Placement of Ammodytidae within Perciformes is a phylogenetic assumption which has never been adequately tested partially due to lack of defining synapomorphies for perciform fishes. Monophyly of Perciformes is questionable since they share no known synapomorphies (Johnson and Patterson 1993, Rosen and Patterson 1990, Lauder and Liem 1983, Rosen 1973). A polyphyletic origin for perciform

fishes was suggested by Patterson (1964), but he later (Patterson 1968) recanted his hypothesis based upon a comparative study of caudal skeletons from mesozoic acanthopterygians. A polyphyletic Perciformes was also entertained in certain respects by Greenwood et al. (1966), and Rosen (1973) who felt that perciform taxonomic schemes were apparently formulated as matters of convenience.

Attempts have been made to define perciforms in a general sense (Rosen 1973, Nelson 1984) with character lists but such an approach has serious methodological flaws and thus has been unsuccessful in delineating the order. Critical analysis of these characters basically demonstrate most are symplesiomorphic but they are useful in terms of helping eliminate unproductive research efforts and circumscribing potentially fertile areas of new investigation. Nelson (1984) listed the first thirteen characters and a fourteenth is added which reports on number of oil globules in fish eggs (Ida 1976):

1. Spines in fins.
2. Two dorsal fins, never an adipose.
3. Ctenoid scales or scales absent.
4. Pelvic fins, if present, thoracic or jugular.
5. Pelvic fins with one spine and five soft rays, sometimes fewer.
6. Pectoral fin base lateral and vertical.
7. Upper jaw bordered by premaxilla
8. Swim bladder, physoclistic.

9. No orbitosphenoid.
10. No mesocoracoid.
11. No epipleural ribs.
12. Acellular bone in adults.
13. Principal caudal fin ray number never more than seventeen, often fewer.
14. Usually one oil globule in the eggs, never more than two.

Fin spines occur in most acanthopterygians (Johnson and Patterson 1993), many myctophoids and paracanthopterygians (Rosen 1973). Some assumed perciform families do not have spines in their dorsal and anal fins but this could be secondarily derived. Examples include Ammodytidae, Cepolidae, Channidae, Coryphaenidae, Echeneididae and Icosteidae (Nelson 1984). Paracanthopterygians show a tendency to develop pelvic fin spines (Rosen 1973) and polymixiids have pelvic fin spines (Rosen 1985). Pelvic fin spines are also found in stephanoberyciforms, zeiforms, and beryciforms. Johnson and Patterson (1993) used presence of pelvic fin spines as a synapomorphy for Acanthopterygii. It is thus obvious that fin spines have a wider more primitive distribution than Perciformes

Pelvics in a thoracic or jugular position are not unique to perciforms either since Paracanthopterygians exhibit pelvics in a jugular positions (Rosen 1973) and many myctophiforms and synodontids display subthoracic pelvics (Johnson 1992). A vertically aligned pectoral fin base is

not singularly present in perciforms either because myctophiforms and synodontids demonstrate the advanced state of high set pectorals (Rosen 1973). Upper jaw bordered by the premaxilla and absence of mesocoracoid is found in many primitive neoteleostean (Rosen 1973). Paralepidids and alepisauroids lack mesocoracoids but remain relatively plesiomorphic due to primitive placement of pelvics in abdominal position and pectorals low on flank (Rosen 1973). Loss of orbitosphenoid is observed in paracanthopterygians, stephanoberyciforms, zeiforms and percomorphs (Johnson and Patterson 1993). Epipleural ribs are absent from all recent acanthomorphs (Johnson and Patterson 1993). A physoclistic swim bladder has received virtually no attention in recent papers on acanthomorph, ctenosquamate and percomorph phylogeny (Johnson and Patterson 1993, Stiassny 1986, Lauder and Leim 1983, Rosen 1973) although they were used as a character for Acanthopterygii, by Greenwood *et al.* (1966). Acellular bone occurs in more primitive clades such as Salmonidae, osmeroids and stomiiforms (Rosen 1985). Ida (1976) believed number of oil globules could be a defining character for perciforms because Mito (1960) found eggs of perciforms usually have only one globule and no reported perciforms (Mito 1963) have more than two globules. However, Mito (1963) also found that eggs of some phylogenetically more primitive groups such as gadids and lophiids have one oil globule. Johnson and Patterson (1993)

used seventeen (I,8,7,I pattern) or less principal caudal-fin rays to define Percomorpha. Seventeen principal caudal-fin rays is the only character in above list which is synapomorphic for a group less inclusive than Acanthomorpha but it is not a synapomorphy for Perciformes.

Roberts (1993) showed that current usage of term 'ctenoid scale' encompasses a wide variety of scale types including spinoid, peripheral ctenoid and transforming ctenoid. He used transforming ctenoid scales as the sole synapomorphy supporting monophyly of Percomorpha, which contained three orders, Scorpaeniformes, Pleuronectiformes and Perciformes. Johnson and Patterson (1993) accepted Roberts' character but expanded the limits of Percomorpha to include atherinomorphs, gasterosteiforms, synbranchiforms and tetraodontiforms. They explained that, despite absence of transforming cteni, other evidence supports placement of last four taxa in Percomorpha. The fact that some mugiloids have transformed ctenoid scales (Lui and Shen 1991) provides additional evidence, although not overwhelming, for Johnson and Patterson's (1993) hypothesis of Percomorpha being composed of smegmamorphs (Synbranchoidei, Mastacembeloidei, Ellassomatidae, Gasterosteiformes, Mugilomorpha and Atherinomorpha) and perciforms. Of course this conclusions hinges on evidence that mugiloids are more closely related to atherinomorphs than perciforms (Stiassny 1990, 1993, Johnson and Patterson 1993). Widespread occurrences of

cycloid scales or scales without transforming cteni in percomorphs (Roberts 1993, Johnson 1984) are considered secondarily derived while frequent appearances of cycloid scales at this phylogenetic level has not been considered symptomatic of a poly- or paraphyletic Percomorpha (Johnson and Patterson 1993).

Ammodytidae exhibit these supposed perciform characters: absence of mesocoracoid, orbitosphenoid, epipleural ribs and presence of high set vertically aligned pectorals, one oil globule in egg, seventeen principal caudal fin rays, upper jaw bordered by premaxilla and pelvic fins in a jugular position on only genus that has them, *Embolichthys*. The family lacks fin spines, two dorsal fins, swim bladder and transforming ctenoid scales although there is evidence of spine tip amputation on some scales, a specialization characteristic of transforming ctenoid scales (Hughes 1981, Roberts 1993). Nevertheless, utilization of any of these characters to define perciforms exemplifies employment of uninformative symplesiomorphies for phylogenetic reconstruction, a practice that has been thoroughly discredited as methodologically unsound (Hennig 1966, Wiley 1981, Rosen 1973). Alternatively, Nelson's (1984) list could be interpreted as an inventory of characters which taken collectively define a perciform. That may be true but there is no theoretical or cladistic justification for defining groups on the basis of sharing a

complete or partial set of plesiomorphic characters. Such an approach would be, as Rosen and Patterson (1969, p. 362) so eloquently put it, '... an example of the ultimate futility of using assemblages of primitive characters to express relationship, with large, catch-all basal groups in effect defined arbitrarily by specializations they do not have (Percoidei), leaving many derived and specialized groups of high rank and of uncertain relationships with one another and with basal groups.'

Figure 1a is a recent cladogram obtained from work of Johnson and Patterson (1993) who studied ctenosquamate interrelationships and defined percomorphs with some new synapomorphies. Figure 1b demonstrates how *Embolichthys mitsukurii*, the most primitive ammodytid (Pietsch and Zebatian 1990, *Ida pers. comm.*, Figs. 138-140) fits into their phylogeny and alters tree topologies. Thirty nine characters were used by Johnson and Patterson (1993) and these same characters were checked in *Embolichthys mitsukurii*. Weighing and ordering of characters was exactly the same as their Figure 25 (Fig. 1a). The cladogram of Figure 1b is a strict consensus tree (length 105, CI=.56, RI=.69) of four cladograms (length 98, CI=.60, RI=.74) calculated with the branch and bound option of PAUP. *Embolichthys* comes out in a tetrachotomy with *Percopsis*, stephanoberyciforms and a monophyletic clade comprised of representative taxa from zeiforms, beryciforms and

percomorphs. Synapomorphies which characterize a group comprised of *Melamphaes*, *Embolichthys*, zeiforms, beryciforms and percomorphs are five or fewer hypurals and second ural centrum fused with PU1 + U1. However, not all beryciforms have these two states illustrated by their absence in *Hoplostethus* (Johnson and Patterson 1993). *Embolichthys* also shares the basioccipital origin of Baudelot's ligament with beryciforms, perciforms and *Elassoma* (Fig. 1b). The ligament arises on the exoccipital in zeiforms (Johnson and Patterson 1993). This analysis illustrates how systematically tenuous Ammodytidae are within Percomorpha, as well as weaknesses inherent to current higher level acanthomorph phylogenies due to homoplasy and absence of synapomorphies for major groups.

The large amount of homoplasy, acknowledged by Johnson and Patterson (1993), could partially explain why *Embolichthys* appears in this position (Fig. 1b) but some plesiomorphic characters states found in *Embolichthys*, indeed place it well outside Percomorpha. Presence of dorsal and anal fin spines, an acanthomorph synapomorphy, and spina occipitalis, an Euacanthomorpha (Acanthomorpha minus Lampridiformes) specialization, are absent in ammodytids. Two characters of Acanthopterygii (Stepanoberyciformes, Zeiformes, Beryciformes and Percomorpha), presence of pelvic spine and anteromedial process of pelvic bone are missing in *Embolichthys*.

Epineurals on neural arch or centra of vertebrae 3-6 and dorsal fin originating behind fourth neural spine place ammodytids outside an unnamed group comprised of Zeiformes + Euacanthopterygii (Beryciformes + Percomorpha).

Synapomorphies for Euacanthopterygii (Johnson and Patterson 1993) not observed in *Embolichthys* include; (alternate state for *Embolichthys* in parentheses) second ventral procurrent caudal ray modified (no modification), ligament from shaft of postcleithrum to posterolateral corner of pelvic girdle (no ligament) and supraneural ending distally in bone (supraneurals end distally in cartilage). The angular bend of supraneurals (Fig. 115) from *Embolichthys* are similar to angle of proximal and distal sections of bona fide pterygiophores. Speculation arises whether these supraneurals are actually pterygiophores, which have lost their rays or spines. If so, they represent a different character state in the analysis (supraneurals absent) and do not apply to Euacanthopterygii. Supraneurals of *Embolichthys* are also unusual in having cartilaginous tips on both proximal and distal ends.

Percomorph synapomorphies (Johnson and Patterson 1993) missing in ammodytids are distal and proximal ceratohyals sutured (separated by cartilage in ammodytids), two halves of the pelvic bones rigidly attached (loosely attached in *Embolichthys*, Fig. 116) and transforming ctenoid scales. Ammodytid scales have posterior field spines but they do not

appear homologous with transforming cteni defined by Roberts (1993). There is evidence of spine tip amputation on many ammodytid scales (Figs. 16, 70, 96), but their spines differ from transforming cteni by being consolidated with matrix of scale plate rather than articulated (Roberts 1993, Hughes 1981). Absence of transforming cteni in ammodytids is not as significant a feature if four field scales are considered a more generalized form of percomorph scales. All transforming ctenoid scales have four fields as do many so called cycloid percomorph scales (Figs. 24, 42, 58, 66, 67, Lui and Shen 1991) and all ammodytids have four field scales (Figs. 16, 70, 96) as well. Hence, many putative cycloid scaled percomorphs share four fields scale morphology with transforming ctenoid scaled percomorphs. A more detailed discussion of four field scales follows in the chapter, **Notes on Percomorph Scales**, but suffice to say that evidence implies four field scales might be a synapomorphy for Percomorpha, although various types of four field scale appear sporadically in more primitive taxa.

Three characters from Johnson and Patterson's (1993) analysis strongly imply an ammodytid-percomorph alignment: seventeen principle caudal fin rays, rod-like interarcual cartilage (Figs. 103-111) and loss of free pelvic radials. The seventeen principle caudal fin rays found in *Embolichthys* also occurs in many percomorphs and zeiforms but is strongly suggestive of a percomorph affinity.

Eighteen or 19 were found in representative beryciforms, stephanoberyciforms, polymixiids and veliferids (Johnson and Patterson 1993). Travers (1981) surveyed the distribution of all cartilaginous structures between epibranchial one and pharyngobranchial two and, while finding a rod-like morphology common in percoids and widespread in percomorphs, he concluded it was a synapomorphy for the Ctenosquamata (*sensu* Rosen 1973) because of its mosaic distribution in myctophids, paracanthoterygians, atherinomorphs and percomorphs. If ammodytids are not percomorphs, a rod-like interarcual cartilage in *Embolichthys* is not at odds with Travers interpretation but does not agree with Johnson and Pattersons (1993) suggestion that the rod-like morphology is a synapomorphy for Percomorpha. However, if Travers' interpretation is wrong, and the various types of interarcual cartilages he believed were homologous, actually arose independently, then ammodytids could be percomorphs. Lack of free pelvic radials (Johnson and Patterson 1993) was treated as a synapomorphy for the Percomorpha but the loss of radials in *Embolichthys* is not inconsistent with a placement outside the Percomorpha if the loss is interpreted as parallelism due to overall degeneration of the ammodytid pelvic girdle. Alternatively, the loss may not have anything to do with pelvic girdle reduction and instead suggests ammodytids are percomorphs.

The Ammodytid Pelvic Girdle

Comparison of the pelvic girdle of *Embolichthys mitsukurii* to the typical percomorph pelvic girdle described by Stiassny (1990) tends to remove ammodytids from consideration as percomorphs. The genus *Embolichthys* is partly characterized by pelvic fins (Jordan 1903), although the pelvic girdle is greatly reduced (Figs. 3, 116, 117; Pietsch and Zebatian 1990, fig. 16). Ida (pers. comm.) described the girdle of *E. sarisa* as being more highly developed than *E. mitsukurii* but provided few details to support this observation. The rarity of *E. sarisa* specimens has hindered examining its girdle in the meticulous detail necessary for a definitive study but lateral X-ray of *E. sarisa* (ANSP 113091) (Fig. 17a) reveals a structural form that could not be distinguished from *E. mitsukurii*, although this is obviously only one limited anatomical view. For now, analysis of pelvic osteology for *E. mitsukurii* must be extrapolated to *E. sarisa* until new material becomes available for study.

The percomorph pelvic girdle is typically united along its midline forming one unit with a sutural union on the posterior end and expanded medial plates. Frequently, there are two small anteromedial bony prongs. These derived pelvic morphologies were common to all percomorphs examined by Stiassny (1990) and proposed as synapomorphies for the

clade. Later, Stiassny (1993) used the following synapomorphies for Percomorpha: 1. Posterior sutural union of pelvic girdle halves. 2. Ventrally displaced anterior processes. 3. Inter-pelvic ligament connects pelvic girdle halves (Stiassny and Moore 1992).

Embolichthys lacks anteromedial bony prongs, a posterior sutural union of pelvic halves (Figs. 3, 116, 117) and inter-pelvic ligament. It does show somewhat expanded medial plates, although their degree of opposition in midline is hard to judge as homologous with the typical percomorph condition (Stiassny 1990, fig. 13, Stiassny and Moore 1992, figs. 1, 13, Stiassny 1993, fig. 3). Hence, the morphology that we observe in *E. mitsukurii*, raises doubts about placement of ammodytids within Percomorpha. However, here again the degenerate nature of its pelvic girdle could explain why anteromedial bony prongs, posterior sutural union, and inter-pelvic ligament are absent.

Ligamentous attachment of pelvic girdle to cleithrum is observed in *Embolichthys mitsukurii* and was suggested as possible percomorph synapomorphy (Stiassny and Moore 1992). However, a similar attachment occurs in lampridiforms and they are currently considered basal acanthomorphs (Olney et al. 1993, Johnson and Patterson 1993).

Trachinoid and Ammodytid Relationships

Recently, Pietsch and Zebatian (1990) proposed a phylogenetic relationship of Ammodytidae with trachinoid fishes some of which were used as the outgroup in this study. Trachinoids have been considered a perciform subgroup (Greenwood *et al.* 1966, Nelson 1984) and a few traditional trachinoids such as the Trichonotidae, Uranoscopidae and Trachinidae have been included in Blennioidei, a suborder of Perciformes (Lauder and Leim 1983). Some trachinoid fishes have behavioral and gross morphological similarities with ammodytids including sand burrowing behavior, pelvics with a reduced number of rays and an elongate eel-like shape. However, monophyly of the trachinoids and their relationship to other perciform groups is unclear. Pietsch (1989) pointed out that families placed in the trachinoid assemblage by Nelson (1984) and Watson *et al.* (1984) are similar to those discussed by Günther (1861) and Gill (1862b), but the former two authors believed that their interpretation of Trachinoidei was polyphyletic. Pietsch's (1989) Trachinoidei were selected from all families previously or currently considered trachinoid because, 'they appear to have cladistic affinity' (Pietsch 1989, p. 259) but there are some problems with Pietsch's phylogeny. For example, Mooi and Johnson (1993) found

evidence to align the Champsodontidae with scorpaeniforms based upon the morphology of epaxial musculature and presence of a parietal sensory canal. They believed that removal of Champsodontidae from Trachinoidei creates uncertainty concerning integrity of a trachinoid assemblage and believed that Trachinoidei as currently defined by Pietsch and Zebatian (1990) should be dismantled.

Closer scrutiny of Pietsch and Zebatian's (1990) characters and hypothesis indicate that relationship of Ammodytidae to some trachinoids is equivocal as well as interrelationships of trachinoids. Johnson (1993) pointed out that Ammodytidae lack the two characters used to define the entire trachinoid clade: pectoral radials small, short and wide and possession of a pelvic spur. Homology of the pelvic spur of *Embolichthys* (Pietsch and Zebatian 1990, fig. 16, Figs. 3a, 3b, 116, 117), pictured as a rather inconspicuous bump, is certainly questionable when compared to the prominent spur observed in other trachinoids (Pietsch 1989, fig. 3). In addition, some of Pietsch and Zebatian's (1989) synapomorphies for the Leptoscopidae, Ammodytidae, Uranoscopidae and Trachinidae clade and Ammodytidae, Uranoscopidae and Trachinidae clade (Fig. 2a) are not present in the putatively most primitive ammodytid, *Embolichthys mitsukurii*, nor *Bleekeria* and *Gymnammodytes*. Revised analysis of trachinoids with addition of all ammodytid genera (Fig. 2a, 2b, Tab. 7, see 'Selection of

Outgroups') radically changes certain aspects of Pietsch and Zebatian's (1990) phylogeny especially relationships of less derived trachinoids.

Epidermal covering united between scales and absence of hypobranchial tooth plates were synapomorphies for a clade comprised of Leptoscopidae, Ammodytidae, Trachinidae and Uranoscopidae (Pietsch and Zebatian 1990). Only two genera of ammodytids, *Ammodytes* and *Hyperoplus* (Fig. 4a) have epidermal covering united between scales and thus independent derivation in these two taxa is more parsimonious than employing the character as a synapomorphy for the entire clade. *Embolichthys mitsukurii* has tiny toothplates on its hypobranchials (Fig. 118) while absence of hypobranchial toothplates has been reconfirmed in all other genera of ammodytids. Therefore, independent loss of toothplates at the more derived node above *Embolichthys* (Fig. 2a) offers an alternative interpretation of this character's distribution and is thus not necessarily a synapomorphy for the family

The following specializations were used to define a monophyletic Ammodytidae, Trachinidae and Uranoscopidae (Pietsch and Zebatian 1990): extrascapulars large and well ossified, hyohyoidei adductores muscle with anterodorsal section greatly restricted, lateral line turning ventrally and extending out on to the middle rays of the caudal fin, scales forming discrete oblique rows, scales at right angle

to oblique rows, sphenotic with a lateral posteroventrally directed process, epiotic with posterolateral expansion, posterior most infraorbital fused to cranium, cutaneous axillary appendage above pectoral fin and entire length of dorsal fin lying in a deep groove (Pietsch and Zebatian 1990). Some of these assumed synapomorphies have a wider distribution in other so called trachinoids, homology of others can be refuted on morphological grounds and a few are homoplastic, being found only in more derived ammodytids.

Large well ossified extrascapulars (*Embolichthys mitsukurii*, Pietsch and Zebatia 1990, fig. 2) and greatly restricted anterodorsal section of the hyohyoidei adductores muscle (*E. mitsukurii*, Fig. 121) also occur in *Trichonotops* *Trichonotops multistriatus*, and *Trichonotops* sp. 1 and 2 (Figs. 120, 122). Course of the lateral line on trunk may be an indicator of relationships but a wider survey of this morphology is also suggested in order to assess the phylogenetic implications of its distribution (Webb 1989b). Absence of a sphenotic process in uranoscopids does not make it the strongest synapomorphy for ammodytids, trachinids and uranoscopids but its use is justified (Pietsch and Zebatian 1990) on the basis of parsimony. Reconsideration of Pietsch and Zebatian's (1990) epiotic expansion character reveals that more similarities exist in the epiotic expansions of ammodytids (Fig. 119), uranoscopids (Pietsch 1989, figs. 10, 11, Pietsch and Zebatian 1990, figs. 2, 3) and trichonotids

(Fig. 120) than trachinids (Pietsch 1989, fig 8). The former three have processes which are reduced shelves or small triangular knobs and do not compare to the exaggerated plesiomorphic epiotic expansion of trachinids (Pietsch 1989, fig. 8).

The posteriormost infraorbital of uranoscopids is indeed fused to the cranium but it is flush with cranial bones between the sphenotic and frontal (Pietsch 1989, fig. 10). It is hard to detect in trachinids (Pietsch 1989, fig. 8) but lies flat against the cranium over the sphenotic. *Embolichthys mitsukurii* indeed exhibits fusion of posteriormost infraorbital to sphenotic but it is limited only to the dorsomedial rim. Its tubular infraorbital protrudes ventrally from the sphenotic and does not lie flat against cranial bones (Pietsch and Zebatian figs. 2, 3, Fig. 119). Fusion is not universally present in all ammodytid either since it does not occur in *Hyperoplus*, *Ammodytes* and *Gymnammodytes*. Infraorbitals of trachinids and uranoscopids (Pietsch 1989, figs. 7, 17) are wider and more sculpted than the narrow tubular infraorbitals of ammodytids (Pietsch and Zebatian 1990, fig. 7) or trichonotids (Nelson 1989, fig. 1). Uranoscopids, trachinids (Pietsch 1989, figs. 7, 17) and trichonotids (Nelson 1986, fig. 1) also have a complete series of infraorbitals while ammodytid infraorbitals are incomplete (Gosline 1963, fig. 2) although *E. mitsukurii* apparently is missing only one (Pietsch and Zebatian 1990,

fig. 7). Consequently, homology of ammodytid, uranoscopid and trachinid posterior most infraorbital fusion is not accepted because of wide difference in infraorbital orientation, shape, presence or absence of bones in infraorbital series and type of fusion of posterior most infraorbitals to cranium.

Finally, *Embolichthys*, *Bleekeria* and *Gymnammodytes* do not have scales in oblique rows which was employed as a synapomorphy for ammodytids, uranoscopids and trachinids (Pietsch and Zebatian 1990). *Embolichthys mitsukurii*, Pietsch and Zebatian's (1990) plesiomorphic representative of the family and *Bleekeria* have overlapping scales. *Gymnammodytes* is naked anteriorly and exhibits widely dispersed scales on posterior half of body and caudal peduncle (Fig. 4b). With all ammodytid genera added to analysis (Fig 2a), presence of oblique scales rows is more parsimoniously understood as an independent derivation in two subgroups; uranoscopids - trachinids and *Hyperoplus* - *Ammodytes* (Fig. 2b).

Johnson (1993) recognized the node for Ammodytidae, Uranoscopidae and Trachinidae was strongly supported by large number of characters (Pietsch and Zebatian 1990) but careful review has diminished that support. To summarize, the following specializations remain: lateral line turning ventrally and extending out on to the middle rays of the caudal fin, sphenotic with a lateral posteroventrally

directed process (lost in uranoscopids), fleshy axillary appendage over pectoral fin and entire length of dorsal fin in a deep groove. Due to the absence of corroborating osteological evidence the cutaneous axillary appendage and entire length of dorsal fin lying in a deep groove are curious synapomorphies for the clade (Pietsch and Zebatian 1990). Nevertheless, their occurrence and homology are difficult to refute and remain strong testimony for integrity of this group.

Further proof of relationship between trachinids, uranoscopids and ammodytids comes from morphological similarity of their otoliths (Gaemers and Schwarzhans 1973, Gaemers 1984, Nolf and Lapierre 1976, Nolf 1978, Menzel 1980, 1983). Nolf (1993, fig. 10) presented data demonstrating that otolith morphology defended sister group relationship of Ammodytidae to Uranoscopidae and Trachinidae. All have otoliths which are elongate and massive with a narrow sulcus composed of an equally wide ostium and cauda. There was no way to link their otoliths with those from other trachinoids because other trachinoids have otolith morphologies that are either autapomorphic or typically percoid.

New information profoundly influences trachinoid - ammodytid phylogeny (Figs. 2a, 2b, Tab. 7). Trichonotids, leptoscopids and sand eels in the genera *Ammodytes*, *Hyperoplus* and *Gymnammodytes*, have a modified elongate

terminal lateral line scale at base of caudal fin (Figs. 18, 19, 20). Trichonotids and leptoscopids show the scale with an enclosed canal (Figs. 18, 19) while the ammodytid version exhibits an open perforated groove (Fig 20). Ammodytids, uranoscopids and trichonotids possess a dorsally directed process on their interoperculars (Figs. 111-114). Trichonotids and ammodytids share highly elongate anterodorsal process of the suboperculum (Figs. 113, 114), supraoccipital osteology with a greatly reduced crest and posterolateral wings of laminar bone (Fig. 115) and scales with posterior field radial ridges ending in blunt spines on posterior margin (Figs. 12, 13, 16).

Phylogenetic analysis with new and revised data (Fig. 2b) does not alter the relationships of Ammodytidae, Trachinidae and Uranoscopidae but resolution of other families is greatly diminished reflecting their lack of cladistic affinity. The restricted hyohyoidei adductores muscle, well ossified extrascapulars and small process on interopercular (lost in trachinids) unites trichonotids with uranoscopids, trachinids and ammodytids contrary to the presumed closer affinity of trichonotids to percophids and creediids (Pietsch 1989, Pietsch and Zebatian 1990). The nature of ammodytid, trichonotid, trachinid and uranoscopid relationships remains to be elucidated. Similarities in scale lepidology, supraoccipital and subopercular osteology insinuate a closer relationship between ammodytids and

trichonotids whereas fleshy axillary appendage over pectoral fin and entire length of dorsal fin in deep groove point to an alternative closer affinity with uranoscopids and trachinids.

Johnson (1993) stressed that osteological characters from gill arches, median fin supports, supraneurals, intermuscular bones and caudal skeleton, should be investigated in order to clarify trachinoid - ammodytid relationships. Comparison of gill arches from *Trichonotops* and *Embolichthys* revealed only symplesiomorphic similarity. Both have hypobranchial toothplates (Figs. 118, 123) and serial arrangements (definition of Rosen 1973) of pharyngobranchials (Figs. 103, 104, 124, 125). *Trichonotops* differs from *Embolichthys* in having a more prolonged pharyngobranchial 2 (Figs. 124, 125), epibranchial toothplates and lacks pharyngobranchial 1 and interarcual cartilage ((Fig. 125). Uranoscopid dorsal gill arches are notable for severe reduction or loss of pharyngobranchial 2 (Rosen and Patterson 1990, fig. 36, Pietsch 1989, figs. 27, 29) and a forked hyobranchial 3 (Pietsch 1989, fig. 27). Trachinid arches are similar to those of *E. mitsukurii* except they display a small tooth plate hinged just posterior to main tooth plate of pharyngobranchial 2.

Osteology of the caudal skeleton of ammodytids and trichonotids are very different (Figs. 127, 128). Trichonotids have one epural, ammodytids two. Ammodytids

possess abundant procurrent rays as well as dorsal and ventral sets of cartilages underlying some procurrent rays (Pietsch and Zebatian 1990, fig. 15, Fig. 127).

Trichonotids have only one or two procurrent rays and lack these cartilages (Nelson 1986, fig. 3, Fig. 128).

Trichnotops also shows a curious posterodorsal ossification of hypural 3, creating a gap between part of hypural 3 and all of hypural 4. The caudal skeleton of uranoscopids is unlike ammodytids in having three epurals with second and third supporting four procurrent rays and two completely fused dorsal and ventral hypural plates (Pietsch 1989, fig. 32). Trachinids have a caudal skeleton similar to uranoscopids except the dorsal hypural plate is incompletely fused.

Neural and haemal arches of caudal peduncle in ammodytids and trichonotids are fundamentally different. Trichonotids possess short pungent spines while *Embolichthys* and *Bleekeria* (Fig. 17a, Pietsch and Zebatian 1990, fig. 15, Ida 1976, Fig. 6) have elongate blunt tipped spines and other ammodytid genera exhibit blade-like processes (Fig. 17b, 127). Posterior margins of the anal and dorsal fins terminate over preural centrum 2 in trichonotids, whereas in ammodytids, they end farther forward over preural centra 4 to 12. The posterior margin of dorsal and anal fins end approximately over preural centrum 5 in uranoscopids and trachinids. Uranoscopids, trachinids, trichonotids and the

ammodytids, *E. sarisa*, *E. mitsukurii* and *B. viridianguilla* share one aspect of dorsal fin anatomy in which last two dorsal fin rays articulate on ultimate dorsal pterygiophore. However, this is probably symplesiomorphic since it is observed on other perciforms (Gill and Hoese 1993, Gill and Mooi 1993).

Notes on Percomorph Scales

Scarcity of species of *Bleekeria* and *Embolichthys sarisa* in collections disallowed clearing, staining and radical dissection and necessitated investigation of alternative characters which could help elucidate Ammodytidae phylogeny. One or two scales plucked unobtrusively from the flanks had minimal impact on condition of rare specimens and cursory examination of scales from common ammodytid species uncovered more morphological detail than had been previously inferred when scales were simply described as cycloid (Nelson 1984, Pietsch and Zebatian 1993). Consequently, a scanning electron microscopic examination of scales was initiated and uncovered informative character data, especially on the posterior field. The study demonstrated lepidologies are, except for species *Bleekeria viridianguilla* and *Embolichthys sarisa*, consistent with currently recognized nominal genera. However, there was virtually no data on phylogenetic

significance of many scale structures and initially it was difficult to systematize and polarize scale character data.

There has been a conspicuous lack of phylogenetic data on cycloid scale variation. In fact, use of the term cycloid in systematic works has included a diverse array of scale morphologies. Scales from *Uranoscopus* (Fig. 9), *Trachinus* (Fig. 10), *Embolichthys* (Fig. 12) and *Trichonotops* (Fig. 13) were called cycloid by Pietsch and Zebatian (19990) but closer inspection reveals anterior field scalelets, sulci and posterior field lepidologies which, in the case of *Embolichthys* and *Trichonotops*, are actually spines. Hence, a broad survey of teleostean scales was made, especially the so called cycloid scales of percomorphs in order to better understand phylogenetic significance of complex lepidologies which were previously ignored when employing cycloid as the terminology.

Dividing scales into fields based upon presence of unique lepidological regions and optimizing their variation on cladograms depicting euteleostean relationships, such as one finds in Johnson and Patterson (1993), Johnson (1992), Stiassny (1984) or Rosen (1973, 1985) provides a more coherent picture of scale character transformations. The primitive scale has only concentric ridges (Fig. 29, CONR). True plesiomorphic cycloid scales are thus defined by a series of concentric ridges encircling a round nucleus.

There is no field definition, scalelets or other structural detail (Figs. 28, 29, 31, 33). The predominant scale type found in ostariophysans, salmonoids, osmeroids (Fig. 15) and stomiiforms (Roberts 1993, Steinmetz and Müller 1991, Järvi and Menzies 1936), some paracanthopterygians (Fig. 21) and some aulopiforms (*Parasudis*, Fig. 29) is cycloid.

A survey of percoid families Johnson (1984) listed as having cycloid scales revealed cycloid scales (round scales with only concentric ridges around a simple focus) occur only in: *Rachycentridae* (*Rachycentron canadum*, Fig. 28), *Echeneididae* (*Remora* sp., Fig. 31) and *Coryphaenidae*, (*Coryphaena hippurus*, Fig. 27). The degree of ossification in these scales is reduced although concentric ridges on *Coryphaena* (Fig. 32) show higher intensity of calcification, judged by vividness of alizarin uptake. All carangoid cycloid scales also have reduced numbers of concentric ridges comparable with other more primitive teleostean cycloid scales (Järvi and Menzies 1936; Steinmetz and Müller 1991) suggesting they arose as a result either neotenic or reductive processes. Similar weakly ossified cycloid scales with widely spaced concentric ridges have been observed in the less derived acanthomorphs *Zeus japonicus* (Fig. 33) and *Rheocles sikorae* (Fig. 34).

Exceptions to the general pattern of cycloid scales in basal teleosts was noted by Roberts (1993, figs. 5, 6) for some characiforms and *Gonorynchus* (Fig. 30) which have

spines on their posterior fields. *Gonorynchus* displays anterior field scalelets separated by sulci, a morphology commonly seen in more derived acanthomorphs but also anomalously observed on the esocid *Esox* (Fig. 46) and certain cyprinids (Steinmetz and Müller 1991, p. 15, pl. 3).

Steinmetz and Müller's (1991) atlas of scales from European fishes shows many cyprinids with structural details on their scale plate in addition to concentric ridges. Many cyprinids have folded anterior fields, anterior field scalelets separated by sulci and patterns in the posterior field. The main distinguishing feature of their scales compared to more derived acanthomorphs are scalelets and sulci in the posterior field (Steinmetz and Müller 1991, pls. 5, 12, 16, 25) of cyprinids. The number of anterior sulci and scalelets of some cyprinids are also plentiful but there are less than five primary sulci (sulci with uninterrupted path from focus to anterior margin). Instead they exhibit numerous secondary or partially radial sulci (Steinmetz and Müller 1991, pls. 16, 30). Nevertheless, partial radial sulci, abundant posterior field sulci, absence of anterior field scalelets in intervening groups between cyprinids and myctophids and their primitive placement within Euteleostei based upon other characters (Rosen 1973), suggests that the anterior field scalelets of cyprinids are an independent derivation.

Cycloid scales are thought to be primitive prototypes

for more derived morphologies (Lagler 1937, Roberts 1993). and a scanning electron microscopic study of lateral line canal ontogeny (Webb 1989a) demonstrates an ontogenetic transformation series of flank scales which supports this hypothesis. Scanning electron photomicrographs clearly illustrates that an 11 mm SL specimen of *Cichlasoma nigrofasciatum* (Webb 1989, fig. 2B, p. 56) has cycloid scales much like *Parasudis* (Fig. 29) or *Rachycentron* (Fig. 28) with large focus and concentric ridges. Figures 3A-D of Webb (1989a, p. 58) shows that larger specimens from 14-17.2mm SL have cteni replacing concentric ridges in the posterior field. These photographs are excellent illustrations of an ontogenetic transformation series from primitive cycloid to derived ctenoid lepidologies.

Accessory scales also provide insights into primitive ontogenies which give rise to apomorphic morphologies. Accessory scales of *Chaetodipterus* (Fig. 52) implicate simple cycloid scales in a linear transformation to spined and ctenoid scales (Fig. 51). Cycloid accessory scales have been also found in *Pomatomus* (Figs. 44, 59) revealing that a simple echeneoid like cycloid scale is at least part of the developmental program for *Pomatomus*.

The first modification of concentric ridge patterns appears as folding or scalloping of the anterior (**ANT**) scale field (Fig. 29, **FD**). Hints of field definition are also observed on scales of *Parasudis* (Fig. 29), where there is

some slight folding of the anterior section and a sharp change in direction of concentric ridges between anterior and lateral fields. Folding of anterior field into protoscalelets has been figured by Roberts (1993, fig. 4) for *Megalops atlanticus*, *Cyprinus carpio* and some cyprinids by Steinmetz and Müller (1991). These anterior scale fields are divided by three to five radial ridges with corresponding radial valleys. Concentric ridges are contiguous through the valleys over to the next adjoining radial ridges. The number of anterior field protoscalelets are usually less than five but *Polymixia* (Fig. 37) is an exception. *Polymixia* exhibits numerous folded protoscalelets (**FPS**) in the anterior field alternating with radial valleys (**RV**). Folding thus seems to become progressively more common and numerous in more derived groups. For example compare *Neoscopelus* (Fig. 38), *Holocentrus* (Fig. 39), *Rheocles* (Fig. 34) and *Polymixia* (Fig. 37).

Origin of anterior field sulci and scalelets is a mystery but evidence suggests they arose from folded or scalloped ancestors. Scanning electron micrograph of a scale from *Myctophum* (Fig. 40) illustrates concentric ridges continuing through valleys over to adjacent radial ridges while an alizarinized preparation (Fig. 41) shows the nadir of these valleys are sulci. Perhaps this is a transition state between scalloped or folded anterior fields and

scalelets separated by primary sulci?

Appearance of anterior field scalelets separated by primary sulci parallels the division of scale plate into two fields or regions. Such scales have an anterior field characterized by scalelets and sulci and a combination lateral-posterior field with only concentric ridges. Examples of this type of scale is seen in juvenile mugilids (Liu and Shen 1991, figs. 12A, 14A, 15A, 16A), adult poecilliids (Hollander 1986), cyprinidonts (Fig. 54), trachinoids (*Trachinus*, Fig. 10) and the following percoids: *Siniperca* (Fig. 53), Carangidae (*Caranx*, Fig. 35), Nematistiidae (*Nematistius*, Fig. 36), Centropomidae (*Ambassis*, Fig. 66), Ehippididae (*Ehippus*, Fig. 47), *Chaetodipterus*, (Fig. 51), Percichthyidae (*Acropoma*, Fig. 48), Cepolidae (*Cepola*, Fig. 49), Sciaenidae (*Equetus*, Fig. 50), Enoplosidae (Fig. 64), Pempheridae (Fig. 65) and some serranids (McCully 1961, figs. 85, 88, 100, 107, 110, 113, 116). Many of those percoid scales have been called cycloid (Johnson 1984) but obviously have more morphological structure than primitive cycloid scales (Järvi and Menzies 1936, Figs. 29, 33, 38). Hence, scales from many cycloid scaled acanthomorphs reveal lepidologies which could better be described by considering anterior field scalelets and combined structure in lateral and posterior regions of scale. Consequently the term, two field scale, seems more appropriate than cycloid scale for those acanthomorph

cycloid scales listed above which display anterior field scalelets and concentric ridges in other scale regions.

By themselves anterior field scalelets and sulci demonstrate that a scale is not cycloid because the ridges of anterior scalelets are not contiguous with those of neighboring scalelets nor is there exact continuity with ridges from neighboring fields (Fig. 11). Figure 55 displays the congrogadid condition with extensive scale coverage by radial sulci. The congrogadid scale is not cycloid because concentric ridges do not encircle entire scale from focus to peripheral margin due to interruption by radial sulci. Certainly, the congrogadid condition is derived as perhaps many of these percoid cycloid scales are (Johnson 1984) but they are not cycloid if a consistent definition of cycloid is accepted.

Lateral fields of two field scales generally lack a unique morphology and could best be described as having only parallel or concentric ridges (Figs. 10, 25, 26). However, scales from *Leiognathus equulus* (Fig. 14), *Ambassis* (Fig. 66), *Caranx* (Fig. 35) and *Pempheris* (Fig. 65) share a sharp anterior-posterior angular change in direction of concentric ridges occurring mid-scale dorsoventrally. Phylogenetic significance of this lepidology remains to be determined but suggests that further comparative investigations might prove valuable by uncovering relationships which have been ignored or overlooked.

Some two field and cycloid scaled perciforms may have arisen by a process Roberts (1993) described as alterations in 'developmental trajectories' and carangoid scales tend to substantiate that view. Rachycentridae, Echeneididae, Coryphaenidae, Nematistiidae and Carangidae have been grouped together as the carangoids (Johnson 1984; Smith-Vaniz 1984). Carangoids are osteologically more derived and seem to belong with other percoids (Johnson 1984), which predominantly exhibit four field lepidologies but carangoids display more plesiomorphic cycloid and two field morphologies. Nevertheless, observed scale patterns are consistent with a phylogeny of carangoids hypothesized by Smith-Vaniz (1984) where Nematistiidae are sister group to cycloid scaled echeneoids (Echeneididae, Rachycentridae, Coryphaenidae) and Carangidae (Smith-Vaniz 1984) or sister group relationship of Rachycentridae and Coryphaenidae proposed by Johnson (1984). Rachycentridae have also been mentioned as relatives (Nelson 1984) of Echeneididae. Carangidae and Nematistiidae scales (*Nematistius* Fig. 36, *Caranx* Fig. 35), exhibit two fields with five or fewer anterior scalelets. *Caranx* has concentric ridges that sharply change direction midscale dorsoventrally (Fig. 35) while concentric ridges of *Nematistius* (Fig. 36) follow the scale margin. Occurrence of true cycloid scales in adult echeneids, coryphaenids and rachycentrids, implies that their scales have undergone greater developmental truncation

than the developmentally less restrained two field scales of carangids and nematistiids.

Appearance of greater scale diversity in the posterior field is manifested by scales with four well defined fields. Scales of serranids (McCully 1961; Lagler 1947), percoids (Lagler 1947), mugilids (Lui and Shen 1991) and ammodytids (Fig. 12) provide good examples of this lepidology. Four field scales first appear around the level of "aulopoids" or ctenosquamates (see Rosen 1985, fig. 45) but are not consistently present until the percomorphs (refer to Johnson and Patterson 1993, fig 24). Some exceptions are observed (*Gonorynchus*, Fig. 30) but homoplasy for this morphology is not common. *Aulopus* (Fig. 57) exhibits one of the early types of four field scales with a spiny posterior field and well defined anterior and lateral fields but is notable for absence of anterior field scalelets.

Four field scales can be divided into two categories based upon gross posterior field morphology. One type is characterized by numerous concentric ridge encircling nucleus so that the posterior field does not directly contact the nucleus (Fig. 58). Concentric ridges in posterior regions or fields of cycloid scales, two field scales and mugilids, whose ontogeny indicates transformation from two field juveniles to ctenoid scaled adults (Lui and Shen 1991), provide evidence for hypothesis which interprets concentric ridges in posterior field as plesiomorphic.

Examples of this morphology can be found in mugilids with membranous cteni (Liu and Shen 1991, figs. 6C, 15D, 16B, 21C), some serranid ctenoid scales (McCully 1961, pp. 24, 30, 116, 124) and *Embolichthys sarisa* (Fig. 58). The second category is characterized by wedge shaped posterior field with vertex directly abutting nucleus (Fig. 12). This morphology is considered apomorphic and illustrated by *Cheimarrichthys* (Fig. 25), *Trichonotops* (Fig. 13), *Embolichthys mitsukurii* (Fig. 12), platycephalids (Hughes 1981) and serranids (see page 48, 51, 55, McCully 1960).

The posterior fields of four field percomorph scales exhibits the greatest amount of diversity among teleostean fishes and are relatively untapped reservoirs of phylogenetic information. Elaborate and unique structures adorn this part of the scale, which includes the enigmatic cteni (Figs. 25, 26), spines (Fig. 44), concentric ridges (Figs. 10, 35, 53), radial ridges (Figs. 13, 70-72), variegations (Fig. 24) and membranes (Figs. 58, 66). Major works using scale morphology in phylogenetic reconstruction have concentrated on posterior field variation (McCully 1961, Lui and Shen 1991, Coburn and Gaglione 1992, Roberts 1993). However, most phylogenetic studies which used scale character data in the analysis ignored posterior field diversity and utilized the long accepted but limited character states, cycloid and ctenoid (Pietsch and Zebatian 1990, Johnson 1984, Lauder and Leim 1983, Rosen 1973,

Greenwood et al. 1966).

Percoids including opistognathids, cheilodactylids, chironemids and cirrhitids (*Chirodactylus*, *Threpterus*, Figs. 42, 67) have scales which are called cycloid (Johnson 1984) but they are not cycloid in the strict sense because of their four field lepidologies. They exhibit anterior field scalelets, parallel lateral field ridges and posterior fields with rough, granular ossifications imbedded in a posterior membrane. Concentric ridges continuing from lateral fields are sometimes observed underlying the posterior membrane like matrix. It is unclear whether these scales transformed from ctenoid ancestors but the cycloid description is certainly misleading.

Previously, any ctenosquamate scale with posterior field spines (Rosen 1973) were called ctenoid but new evidence questions the homology of all these spines (Roberts 1993). Spinoid and ctenoid scales have been surveyed by Roberts (1993) and suffice it to say that the appearance of spinoid scales occurs first in some ostariophysans, mainly characiforms (Roberts 1993, figs. 5-7) but start to consistently arise in more derived teleosts at the level of Aulopiformes (Fig. 57). Different types of spines and cteni (Roberts 1993) are the most prevalent structures on the posterior field throughout the so called Ctenosquamata and Roberts used transforming cteni as a synapomorphy for Perciformes. Transforming cteni are small spines which

articulate with connective tissue layer of the scale plate. Anteriorly, from posterior row or rows of marginal pungent cteni, spine tips are amputated or partially resorbed (McCully 1970, Hughes 1981). These bony spines can be disarticulated by chemical hydrolysis of connective tissues (Hughes 1981). Although not an exhaustive list, transforming ctenoid scales can be seen in percichthyids (Figs. 26, 48), sciaenids (Fig. 60), serranids (McCully 1961, 1970), platycephalids (Hughes 1982), some apogonids (Fig. 62), some ephipidiids (Figs. 51, 63), cheimarrichthyids (Fig. 25), pinguipediids (Fig. 56) and various mugilids (Liu and Shen 1991).

Perciform transforming ctenoid scales (McCully 1961, Lanzing and Higginbotham 1974, Roberts 1993) and many cycloid perciform scales (Figs. 24, 42, 53, 61, 67) share two morphological features: 1) division of scale plate into four recognizable regions or fields, 2) anterior field scalelets (Roberts 1993, McCully 1960). Transforming ctenoid scales do not exist without anterior field scalelets but phyletic distribution of anterior field scalelets is hard to assess. Anterior field scalelets appear sporadically in ctenosquamates without transforming cteni (Figs. 30, 43, 46) but four field scales with greater than five anterior field scalelets, pentagonal shape and transforming cteni do not occur simultaneously until Percomorpha, although there are exceptions. Many percoid

'cycloid' scales exhibit less than five anterior scalelets (Figs. 35, 36, 47, 49, 66) and some percoids with transforming cteni have less than five anterior scalelets (Figs. 48, 51, 63). However, no examples of more than five anterior field scalelets were found on fishes more primitive than Percomorpha, except *Gonorynchus* (Fig. 30). Ammodytids clearly exhibit four field scales with greater than five anterior field scalelets (Figs. 70, 96), implying that ammodytids are at least related to some percomorphs because this character complex only occurs in this groups. However here is an example much like Nelson's (1984) character list (see above: Relationship of Ammodytidae to Perciformes) where simultaneous occurrences of character complexes are used to define a clade. Such an approach, explained previously, suffers from problems associated with using symplesiomorphy for phylogenetic inference. Therefore, an ammodytid - percomorph alignment based upon this method of character analysis is not acceptable but the distinctive presence of more than five anterior field scalelets in Percomorpha, with only a few exceptions, suggests that ammodytids are percomorphs.

Lui and Shen's (1991) color photographs of juvenile and adult mugilid scales revealed most species have juvenile ontogenies with two field scales and adults from the same species display four field scales (Lui and Shen 1991, figs. 2, 5, 6). Their study seems to indicate that, at least in

mugilids, two field scales are primitive relative to four field scales because they appear earlier in ontogenetic sequence. The sciaenid *Otolithes* (Fig. 60) illustrates that a two field substructure underlies expression of a small patch of transforming cteni further implicating two field scales in a transformation series preceding four field lepidologies.

Liu and Shen (1991) hypothesized that membranous cteni were intermediate between mugilid species with two field scales and those with ctenoid four field scales. However, their photographs of scale ontogenies do not substantiate their transformation series hypothesis because no species with adult ctenoid scales has membranous cteni on smaller, developmentally immature individuals (See their figures 15, 16, pp. 340 - 341). Ontogenetically membranous ctenoid and transforming ctenoid scales appear to arise independently from a common two field ancestor. Thus, Liu and Shen's (1991) photographs reveal two field scales are prototypes of more advanced scale varieties including ctenoid, membranous ctenoid and granulated posterior field scales.

Johnson (1984) felt cycloid scales of percoids were secondarily acquired but an alternative hypothesis can explain derivation of these widely misunderstood scales. In some cases simple loss of transforming cteni on the posterior field explains the observed lepidologies. By regarding scale fields as independent units of character

variation, simple loss of transforming cteni from the posterior field is a more parsimonious hypothesis than postulating reversal of an entire scale to cycloid, which is frequently implied when scales are designated cycloid. Scales of *Tilapia mossabica* illustrate this point. They have been labeled cycloid (Lanzing and Higginbotham 1974) but their four field lepidology without cteni and frequent occurrence of ctenoid scales in closely related species clearly indicate their scales originated by loss of cteni from the posterior field. Hence, use of the term cycloid for scales of *T. mossabica* is misleading because its lepidolgy is more derived than primitive cycloid scales displayed by *Parasudis* (Fig. 29) or salmonids (Järvi and Menzies 1936), which basically show only concentric ridges and little or no field definition. The apogonids, *Apogonichthys* (Fig. 61) and *Gymnapogon* (Fig. 62), also suggest that an amorphous posterior field (Fig. 61) is derived from a ctenoid four field ancestor (Fig. 62).

Studies of mugilid (Lui and Shen 1991) and perciform (Webb 1989a) scales ontogenies were combined with plots of scale character states (concentric ridges, less than five anterior field scalelets, greater than five anterior field scalelets, posterior fields with ornamentation such as cteni etc.) on phylogenetic trees (Johnson and Patterson 1993, Johnson 1992, Stiassny 1984, Rosen 1973, 1985). Data was obtained from many examples (Figs 11-16, 21-67) and is

summarized in the following transformations series hypothesis.

Cycloid Scale (concentric ridges no field definition) ---
-----> Two Field Scales (anterior field scalelets and
combination lateral-posterior field with concentric
ridges) -----> Four Field Scales (anterior field
scalelets less than five, lateral field of concentric
ridges, diverse posterior field morphologies) ----->
Four field Scales with greater than five anterior field
scalelets.

Scales of Trachinoid and Ammodytidae

Monophyly of trachinoids and the trachinid, uranoscopid and ammodytid subgroup has been hypothesized by Pietsch (1989) and Pietsch and Zebatian (1990) but the perplexing variation of trachinoid scales exposes the vulnerability of these hypotheses. Figures 9 and 10 show scales of *Uranoscopus japonicus* and *Trachinus vipera*, representative members from Trachinidae and Uranoscopidae, Pietsch and Zebatian's (1990) sister group to Ammodytidae. *Trachinus* has two field scales which are commonly found in many percoids, (Figs. 35, 36, 47-50, 53, 63-66), poeciliids (Hollander 1986) and cyprinodonts (Fig. 54). Uranoscopids are autapomorphic in lacking an enclosed nucleus and having a highly compressed posterior field (Fig. 9). Little similarity exist between these scales and those of Ammodytidae (Figs. 70, 96) except anterior field scalelets which is not a relevant synapomorphy at this hierarchical phylogenetic level.

Comparison of scales from other trachinoids: Cheimarrichthyidae, *Cheimarrichthys* (Fig. 25); Pinguipedidae (*Pinguipes*, Fig. 56); Champsodontidae (*Champsodon* sp., Fig. 8); Trichonotidae (*Trichonotops* sp., Fig. 13); Percophidae (*Bembrops*, Fig. 22); Creediidae (*Limnichthys*, Fig. 102) and Leptoscopidae (*Leptoscopus*, Fig. 24) reveals no common attributes uniting them except anterior field scalelets.

Cheimarrichthys (Fig. 25) and *Pinguipes* (Fig. 56) are clearly in the category of transforming ctenoid (Roberts 1993) while percophid scales (Fig. 22) could be more accurately termed peripheral ctenoid (Roberts 1993). The creediid *Limnichthys* (Fig. 102) has variegated posterior fields, similar to *Leptoscopus* (Fig. 24). These scale are comparable to anodont or toothless posterior field scales of *Epinephelus fasciatus* and *Mycteroperca falcata* (see McCully 1961, pp. 113 & 120). Scales from *Champsodon* (Fig. 8) are unique and resemble no other trachinoids I have examined but do have some superficial resemblance to the thorny crown shape spicules found on epithelium of larval *Coryphaena* and *Rachycentron* (Johnson 1984, figs. 263, 264). Collette (pers. comm.) said the scales of *Champsodon* reminded him of 'caducous' scales on midventral line in males of the darter genus *Percina*, which is a synapomorphy for the genus.

The only apparent homology between ammodytids and trachinoids is found on the posterior fields of trichonotids (Fig. 13) and ammodytids (Figs. 11, 12, 96, 97). They exhibit a network of concentric and radial ridges which end as posterior marginal spines. However, the posterior field margins (Fig. 13) of trichonotids meet at a more acute angle than ammodytids (*Embolichthys mitsukurii*, Fig. 12) and the middle of trichonotid posterior field is distinguished by a narrow wedge of secondary scalelets and sulci (Figs. 13, 97, SSC). Scales from *Trichonotops* also have lepidonts on

anterior field ridges (Figs. 93, 94), a symplesiomorphy they share with *Embolichthys* (Fig. 84) and some species of *Bleekeria* (Fig. 87).

Embolichthys and *Bleekeria viridianguilla* (Figs. 12, 70) have similar scales with respect to their pentagonal shape, four clearly defined symmetric fields and posterior field radial ridges. Scales of other species in the genus *Bleekeria* (Figs. 71, 72) are round or elliptical and exhibit a unique field pattern, characteristic of what appears to be a completely different lineage than *B. viridianguilla*. Grooved sulci are observed only in *Embolichthys* (Figs. 12, 58) and *Bleekeria* (Figs. 70-72) but width of sulci are increased in *Bleekeria*. In this respect *B. viridianguilla* has some similarity with other species of *Bleekeria* as it has wider sulci than *Embolichthys* (compare Figs. 12, 70) but not as wide as the remainder of *Bleekeria* clade. Grooved sulci are widespread in percomorphs and outgroup (Figs. 9, 10, 13, 24-26) which support other data (overlapping scales, tightly packed anterior field scalelet ridges) indicating overall plesiomorphy of *Embolichthys* and *Bleekeria viridianguilla* scales. In all other ammodytids anterior scalelets are separated from adjacent ones by tubular like primary radial ridges (Figs. 73-77, 95) which perforate the concentric ridge surrounding the nucleus (Fig. 79). Such structures are termed **anterior field radial ridges** (Fig. 11, **AFRR**). Anterior field radial ridges are synapomorphic for

Ammodytes, *Hyperoplus* and *Gymnammodytes*.

Two primitive characters observed in *Embolichthys* and *Bleekeria viridianguilla* tend to be linked with narrow sulci. One, is scales with pentagonal shape (Figs. 12, 58, 70) and the second is closer spacing of anterior field scalelet ridges (Fig. 12, **AFSR**). Both features are commonly observed in many percomorphs (McCully 1961, 1970, Hughes 1982, Liu and Shen 1991). Number of anterior scalelet ridges in *B. viridianguilla* (Fig. 70) is slightly less compared to *E. mitsukurii* (Fig. 12) but other sand lances exhibit even greater distance between ridges in their anterior field scalelets. They have an approximate correspondence, ignoring punctuating gaps created by anterior field radial ridges, with concentric ridges of lateral and posterior fields (Figs. 66-69, 70-75, 77). Cursory observation has interpreted these ridges continuously encircling entire scale and was probably the primary reason why ammodytid scales have been mistakenly designated cycloid (Pietsch and Zebatian 1990, Nelson 1984).

Tiny tooth like denticulations, teeth or beads occur on anterior field ridges in *Embolichthys* (Figs. 83-85) and some species of *Bleekeria* (Figs. 86, 87). Many body scales of *Embolichthys mitsukurii* are not heavily beaded or lack lepidonts such as scales from mid-flank (Fig. 68). *Bleekeria viridianguilla* has pungent teeth (Fig. 86) much like *E. mitsukurii* but because denticles are plesiomorphic

(as are their shared similarity of pentagonal shape, anterior field sulci and closely space anterior field scalelet ridges) they are not evidence that *B. viridianguilla* is more closely related to *E. mitsukurii* than other *Bleekeria* species. A transformation series from possession of pungent lepidonts to progressive reduction and loss of can be traced from *Embolichthys* - *Bleekeria viridianguilla* thru *B. rennei* - *B. gilli* to *Ammodytes*, *Hyperoplus* and *Gymnammodytes* (Figs. 83-91). Consequently, loss of lepidonts among Ammodytidae is consistent with a phylogeny based upon total evidence (Fig. 2b, 139) and suggests that their loss defines a derived subgroup within the family, consisting of *Ammodytes*, *Hyperoplus* and *Gymnammodytes*.

Round or elliptical scales seem to characterize a more derived subgroup within Ammodytidae comprised of *Ammodytes*, *Hyperoplus*, *Gymnammodytes* and *Bleekeria rennei*, *B. gilli* (Figs. 11, 73, 74, 79, 71, 72, 95). There is some distortion in field symmetry of all ammodytid scales (Figs. 73, 74) scales but it is more pronounced in rounded or elliptical scaled ammodytids, reaching a zenith in *Bleekeria* (Figs. 71, 72). Contrary to prediction, scales of oblique row species with scales approximately perpendicular to oblique row (*Ammodytes* and *Hyperoplus*, Figs. 73-78), display less field distortion than overlapping scales of *Bleekeria* (Figs. 71, 72). No explanation for these observations can

be made at this time.

Elliptical scales with greatly distorted field symmetry are observed in specimens of *Bleekeria gilli* (Figs. 80, 81) from Cabo San Lucas, Baja California and Galapagos respectively. Another specimen designated *Ammodytes* paratype (USNM 36514) from Hawaii is pictured in Figure 82. This scale also has highly reduced denticles on its anterior scalelet ridges, comparable to *B. gilli* and *B. renniei* (Figs. 87). Despite similarities in shape of some species of *Bleekeria* (Figs. 81, 82) to *A. americanus* and *A. dubius* (Figs. 77, 78), no scales of any species of *Ammodytes* have denticles (Figs. 88, 89) nor the characteristic field distortion (overlapping of posterior field by the ventral lateral field) of this *Bleekeria* subgroup. *Ammodytes* paratype (USNM 36514), *B. gilli* and *B. renniei* (Figs. 71, 72, 81, 82) are clearly related on the basis of their unique lepidology. Hence, *Ammodytes* (USNM 36514) apparently belongs within a *Bleekeria* subgroup not *Ammodytes*.

Compared to other species of *Ammodytes*, flank scales from *Ammodytes hexapterus* and *A. marinus* have heavier, larger, more angular scales with a straight anterior margin (Fig. 75). *Ammodytes tobianus* has smaller elliptical scales elongated dorsoventrally (Fig. 76). The western Atlantic *Ammodytes americanus* and *Ammodytes dubius* (Figs. 77, 78) also display elongation of dorsoventral axis and they seem comparable to scales from *A. tobianus*. *Ammodytes personatus*

(Fig. 79) exhibits scales intermediate between the well ossified more angular scales of *A. marinus* (Fig. 75) and the elliptical delicate scales of *A. americanus* (Fig. 77). Scales from *Hyperoplus* (Fig. 74) display well defined concentric and radial ridges but are more circular in shape compared to some *Ammodytes* (Figs. 75-78), although they are comparable to small specimens of *A. hexapterus* (Fig. 73). *Gymnammodytes* (Fig. 95) has round, extremely delicate scales which stain blue due to apparent absence of ossification and correlate with widespread reduction in body scale coverage (Fig. 4). Their field patterns are similar but less defined than those observed on *Ammodytes* or *Hyperoplus* (Figs. 73-78).

Membranous cteni found on posterior fields of *Embolichthys sarisa* (Fig. 58) are completely different from the posterior field morphology of all other ammodytids (Figs. 11, 12, 16). Scales of *Embolichthys sarisa* are so anomalous that placement of it in *Embolichthys* may not be justified. Ida also questioned their taxonomy when he studied osteology of the pelvic girdle (work in progress). Numerous concentric ridges in the posterior field suggest its scales are primitive (Fig. 58) relative to pattern of wedge shaped posterior field abutting nucleus, characteristic of other ammodytids (Figs. 11, 12, 16). This morphology is also consistent with Ida's proposition that *E. sarisa* is the most primitive ammodytid.

Membranous cteni, strikingly similar to those found on scales of *Embolichthys sarisa* (Fig. 58), are observed on some mugilids (Liu and Shen 1991, figs. 6C, 8A, 11A, 15C). However, *E. sarisa* lacks the focal groove characteristic of these mugilids (Liu and Shen 1991, figs. 6C, 11A, 15C). Most ammodytids examined, except *E. sarisa* and species of *Bleekeria* which are scarce in collections (Robins and Böhlke 1970) and consequently unavailable for dissection, do not possess some of the synapomorphies Stiassny (1990, 1993) interpreted as proof of mugilomorph-atherinomorph affiliation. These synapomorphies are derived from myology and osteology of branchial arches, anterior neural arches, primary and secondary pectoral girdle and fin structure.

The mugilomorph-atherinomorph synapomorphy describing subdivision of pharyngocleithralis muscle and reduction of pharyngohyoideus to a small fan-shaped muscle with an elongate tendon was not pictured by Kayser (1961, figs. 16, 17) for *Ammodytes tobianus*. According to Stiassny (1990), the plesiomorphic ctenosquamate configuration of internal and external levators of branchial musculature has levator externus series originating on postorbital neurocranium and inserting on corresponding epibranchials. Levatores interni originate medially to externus series with levator internus 1 crossing internus 2 and inserting on pharyngobranchial 2. A similar configuration is pictured in the diagram of Kayser for *Ammodytes tobianus* (1961, figs. 15, 17) which

illustrates plesiomorphy of ammodytid branchial arch myology compared to mugiloids.

Homology of atherinomorph-mugilomorph anterior neural arch expansion was questioned by Parenti (1993) and Stiassny (1993) was somewhat compromising on its use as a synapomorphy. In any case, the first neural arch of *E. mitsukurii* (Fig. 126) and *E. sarisa* (Fig. 17) are expanded but homology with the mugilomorph condition (Stiassny 1990, fig. 5) is doubtful because the character applies to expansion of at least three or four anterior neural arches. The dorsal cleithral process of mugilomorphs - atherinomorphs (Stiassny 1993, fig. 11D-H), contrast with the more rounded and extensive ammodytid condition (Pietsch and Zebatian 1990, fig. 16) which is also represented in some non-atherinomorph or non-mugilomorph acanthomorphs (Stiassny 1993, figs. 4B, 11A,B). Stiassny (1993, fig. 7D) also provisionally noted that expansion of the third extrascapular could be supporting evidence of mugilomorph monophyly. *Embolichthys mitsukurii* also displays a somewhat elongate third extrascapular (Pietsch and Zebatian 1990, fig. 2) but its homology with the corresponding mugilomorph extrascapular is questionable since it is not as long. Only one scale character (membranous cteni) from one species of Ammodytidae shared with two genera or five species of mugilids is hardly enough evidence for an ammodytid-mugilomorph alignment and this brief review of mugilomorph-

atherinomorph and mugilomorph synapomorphies indicates that a relationship between mugilids and ammodytids is doubtful. It thus appears membranous cteni arose independently in *Embolichthys sarisa* and some mugilids.

Summary of Characters and States

The plesiomorphic state is represented by zeros.

Character 1: *Multistate character describing morphology of the scale's anterior field.*

- (0) - Greater than five scalelets separated by sulci
- (1) - Greater than five scalelets separated by radial ridges.

Character 2: *Morphology of the posterior field of the scale.*

- (0) - Concentric ridges.
- (1) - Membranous cteni.
- (2) - Concentric ridges and radial ridges formed by truncated spines.

Character 3: *Morphology of the lateral fields.*

- (0) - Possession of parallel or concentric ridges.
- (1) - Secondary ridges present.

Character 4: *Ornamentations found within the last concentric ridge surrounding the nucleus.*

- (0) - Smooth nucleus defined by continuous concentric ridge.
- (1) - Concentric ridge surrounding nucleus broken by anterior field radial ridges.

Character 5: *Shape of the scale.*

- (0) - Pentagonal shaped scales.
- (1) - Round scales.
- (2) - Elliptical scales.
- (3) - Rounding of scale outline with retention of some straight margins.

Character 6: *Lepidonts on the anterior scalelet ridges.*

- (0) - Lepidonts on ridges of anterior field scalelets.
- (1) - Reduced lepidonts on ridges of anterior field scalelets.
- (2) - Absence of lepidonts.

Character 7: *Multistate character which describes the degree of distortion in scale field symmetry.*

- (0) - Well defined field symmetry on a bilaterally symmetric scale.
- (1) - Asymmetry in the shape of the individual fields relative to each other.
- (2) - Gross asymmetry where lateral field extends posteriorly over posterior field contributing to part of posterior margin.

Character 8: *Possession of an elongate terminal lateral line scale which is the caudal extension of the lateral line.*

- (0) - Absence of terminal lateral line caudal scale.
- (1) - Modified elongate lateral line caudal scale with hooded canal.
- (2) - Wide open grooved, modified elongate lateral line caudal scale.
- (3) - Narrow open grooved, modified elongate lateral line caudal scale.

Character 9: *Absence of pelvic fins.*

- (0) - Pelvic fins present.
- (1) - Absence of pelvic fins.

Character 10: *Large oval foramen in the dentary.*

- (0) - No large foramen in dentary.
- (1) - Large foramen in the dentary.

Character 11: *Conspicuous spine like process on the metapterygoid.*

- (0) - Absence of conspicuous spine-like process on the metapterygoid.
- (1) - Presence of spine-like process on the metapterygoid.

Character 12: *Anteriorly directed symphyial process on dentary.*

- (0) - Absences of anteriorly directed symphyial process.
- (1) - Process present.

Character 13: *Multistate character describing the scale patterns on the body flanks.*

- (0) - Overlapping scales.
- (1) - Oblique scale rows with united epidermal covering between scales.
- (2) - Anterior body naked, widely dispersed scales on posterior half of body and caudal peduncle.

Character 14: *A mutistate character describing the absence, presence and extent of ventrolateral skin folds.*

- (0) - Absence of ventrolateral skin folds.
- (1) - Ventrolateral skin folds ends past anterior margin of anal fin.
- (2) - Ventrolateral skin folds end just past tip of pectoral fin.

Character 15: *Complex association of extra cartilages and ossicles in the jaw.*

- (0) - No extra labial ossicles or ligaments.
- (1) - Possession of following ligaments and cartilages: labial, accessory labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, premaxillo-rostral and cartilages IV and V.

- (2) - Full compliment of ossicles replacing ligaments and of cartilages state (1): Labial ossicles 1-6, accessory labial ossicles 1-4, maxillo-dentary ossicle, maxillo-vomerine ossicle, maxillo-premaxillary ossicles 1-3, lateral maxillo-premaxillary ossicle, prerostral ossicle.
- (3) - Possession of following ossicles: labial 6 and 2, maxillo-dentary, maxillo-vomerine, fused maxillo-premaxillary and lateral maxillo-premaxillary, premaxillo-rostral ligament and accessory labial cartilages absent.
- (4) - Same ligaments as state (1) except maxillo-rostral and accessory labial cartilages absent.

Character 16: *Arrangement of pharyngobranchials.*

- (0) - Serial arrangement of pharyngobranchials with lateral displacement of pharyngobranchial two.
- (1) - In line anterior-posterior arrangement of pharyngobranchials.

Character 17: *Scales on the caudal fin musculature.*

- (0) - Scales on the caudal fin musculature.
- (1) - No scales on the caudal fin musculature.

Character 18: *Pigmentation of larval ventral fin membranes.*

- (0) - Pigment present.
- (1) - Pigment absent.

Character 19: *Dorsal body pigmentation of larvae.*

- (0) - Absent.
- (1) - Present.
- (2) - Present and extends to notochord tip.

Character 20: *Ventral body pigmentation of larvae.*

- (0) - Pigment absent or does not extend to tip of the notochord.
- (1) - Post anal pigment extends to the tip of the notochord.

Character 21: *Ventral gut pigmentation.*

- (0) - Ventral gut pigment absent.
- (1) - Ventral gut pigment present.

Character 22: *Caudal pigmentation in small larvae, before 15 mm in length.*

- (0) - Absent.
- (1) - Present.

Character 23: *Position of anterodorsal process of suboperculum relative to operculum and hyomandibula.*

- (0) - Process short, less than one half distance from dorsal margin of subopercular body to

- posterior arm of hyomandibula.
 (1) - Process long, greater than two thirds distance from dorsal margin of the suboperculum to posterior arm of hyomandibula.

Character 24: *Osteology of vomer anterior margin.*

- (0) - Absence of vomerine fangs, vomer pointed.
 (1) - Two fangs, vomer notched.

Character 25: *Osteology of medial maxillary process and maxillary cranial process.*

- (0) - Narrow maxillary medial process and no projection on the maxillary cranial process.
 (1) - Medial maxillary process wide with medial projection on the base of maxillary cranial process.

Character 26: *Structure of the nasal organ.*

- (0) - Organ convoluted with lamellae.
 (1) - Organ smooth and egg shaped.

Character 27: *Diameter of posterior pore of lateral line scale and its location on the scale.*

- (0) - Pore of lateral line scale displaced anteriorly from posterior margin and smaller than canal.
 (1) - Pore as wide as canal and abuts the posterior margin of lateral line scale.
 (2) - No lateral line scales but pores dorsal and ventral to a dermal lateral line.

Character 28: *Dorsal triangular process on the interoperculum.*

- (0) - Process absent.
 (1) - Interopercular process present.

Character 29: *Ossification of extrascapulars.*

- (0) - Extrascapulars absent or small and weakly ossified.
 (1) - Extrascapulars large and well ossified.

Character 30: *Number of extrascapulars.*

- (0) - Possession of more than one extrascapular.
 (1) - One extrascapular present.

Character 31: *Fusion of medial extrascapular to cranium.*

- (0) - Medial extrascapular fused to cranium.
 (1) - Medial extrascapular not fused to cranium.

Character 32: *Myology of hyohyoidei adductores muscle.*

- (0) - Anterodorsal section of hyohyoidei adductores muscle broad.

- (1) - Anterodorsal section of hyohyoidei adductores muscle greatly restricted.

Character 33: *Lateral line morphology.*

- (0) - Lateral line straight, positioned mid-laterally.
- (1) - Lateral line elevated and turning ventrally on caudal peduncle.

Character 34: *Sphenotic with a posteroventrally directed process.*

- (0) - Absent.
- (1) - Present.

Character 35: *Osteology of epiotic expansion.*

- (0) - Epiotics expanded with large wings of bone.
- (1) - Epiotics with small triangular shelf of bone.

Character 36: *Cutaneous axillary appendage associated with the pectoral fin.*

- (0) - Appendage absent.
- (1) - Cutaneous axillary appendage present.

Character 37: *Supracleithrum superficial ossification.*

- (0) - Supracleithrum smooth and covered with thick skin.
- (1) - Supracleithrum superficial, rugose and highly sculptured.

Character 38: *Osteology of neural and hemal spines of caudal peduncle.*

- (0) - Neural and hemal spines of caudal peduncle are elongate and tips pungent.
- (1) - Neural and hemal spines of caudal peduncle are blade-like and wide.

Character 39: *Small shelf of bone projecting anteriorly from the anterior margin of operculum which receives the dorsal tip of the anterodorsal process of suboperculum.*

- (0) - Projecting shelf absent.
- (1) - Projecting shelf present.

Character 40: *Osteology of supraoccipital.*

- (0) - Supraoccipital with prominent posterior crest, anterior process lacking or reduced, prominent deflection of posterior surface as it meets exoccipital.
- (1) - Supraoccipital flat with reduced crest, prominent anterior process and posterolateral extensions of laminar bone.

Character 41: *Entire length of dorsal fin in a deep groove.*

- (0) - Absent.
- (1) - Present.

Character 42: *Scales on the ventral surface.*

- (0) - Absent or scales in tight chevrons on ventral surface.
- (1) - Present.

Character 43: *Scales up to and just anterior to the dorsal fin.*

- (0) - Presence of scales up to and just anterior to dorsal fin.
- (1) - Absence of scales up to and just anterior to dorsal fin.

Character 44: *Number of rays articulating on the ultimate dorsal pterygiophore.*

- (0) - Two rays articulating on the last dorsal pterygiophore.
- (1) - One ray articulating on the last dorsal pterygiophore.

Character 45: *Loss of teeth on the premaxillary and dentary.*

- (0) - Teeth present.
- (1) - Teeth absent.

Table 1: Nominal species and subspecies of *Ammodytes*

<i>Ammodytes alascanus</i> *	Cope, 1873
<i>Ammodytes alliciens</i> *	Lacepède, 1798
<i>Ammodytes aleutensis</i> *	Duncker and Möhr, 1940
<i>Ammodytes americanus</i> *	DeKay, 1842
<i>Ammodytes antipai</i> *	Pauca, 1929
<i>Ammodytes argenteus</i> *	Risso, 1810
<i>Ammodytes capensis</i> 1	Barnard, 1927
<i>Ammodytes cicereus</i> 2	Risso, 1810
<i>Ammodytes dubius</i> *	Reinhardt, 1838
<i>Ammodytes hexapterus</i> *	Pallus, 1811
<i>Ammodytes immaculatus</i> 3	Corbin, 1950
<i>Ammodytes japonicus</i> *	Duncker and Möhr, 1940
<i>Ammodytes kalleolepis</i> *	Günther, 1962
<i>Ammodytes lancea</i> 4	Cuvier, 1829
<i>Ammodytes lanceolatus</i> 5	LeSauvage, 1824
<i>Ammodytes lucasanus</i> 6	Beebe and Tee-Van, 1938
<i>Ammodytes marinus</i> *	Raitt, 1934
<i>Ammodytes personatus</i> *	Girard, 1857
<i>Ammodytes semisquamatus</i> 7	Jourdain, 1879
<i>Ammodytes septapinnis</i> *	Pallas, 1811
<i>Ammodytes siculus</i> *	Swainson, 1833
<i>Ammodytes terebrans</i> *	Cisternas, 1875
<i>Ammodytes tobianus</i> *	Linnaeus, 1758
<i>Ammodytes vittatus</i> *	DeKay, 1842

<i>Ammodytes dubius hudsonius</i>	8	Vladykov, 1842
<i>Ammodytes hexapterus marinus</i>	9	Andriyashev, 1954, Berg et al., 1949
<i>Ammodytes hexapterus murmanicus</i>	10	Lindberg, 1937
<i>Ammodytes lancea dubius</i>	11	Jensen, 1941
<i>Ammodytes lancea marinus</i>	12	Jensen, 1941
<i>Ammodytes tobianus oceanicus</i>	13	Perlmutter, 1940
<i>Ammodytes tobianus japonicus</i>	14	Perlmutter, 1940
<i>Ammodytes tobianus minami</i>	15	Perlmutter, 1940

* - valid

- 1 - Senior synonym of *Gymnammodytes capensis*
- 2 - Senior synonym of *Gymnammodytes cicerellus*
- 3 - Senior synonym of *Hyperoplus immaculatus*
- 4 - Senior synonym of *Ammodytes tobianus*
- 5 - Senior synonym of *Hyperoplus lanceolatus*
- 6 - Junior synonym of *Bleekeria gilli*
- 7 - Senior synonym of *Gymnammodytes semisquamatus*
- 8 - Junior synonym of *Ammodytes dubius*
- 9, 10 - Junior synonym of *Ammodytes hexapterus*
- 11 - Junior synonym of *Ammodytes dubius*
- 12 - Junior synonym of *Ammodytes marinus*
- 13, 14, 15 - Junior synonym of *Ammodytes personatus*

Table 2: Synopsis of Data on North Atlantic Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert.	Dorsal	Anal	Plicae	
<i>A. dubius</i>		Greenland		73	64	33		Reinhardt 1863
<i>A. dubius</i>	coastal, Davis Strait	W.Greenland 60°25'N- 70°40'N		73-80 Avg. 75.1	60-68 Avg. 64.71	30-36 Avg. 33.2		Jensen 1941
<i>A. dubius</i>	offshore	37-69°N NW Atlantic		65-75	56-68	27-35		Richards et al. 1963
<i>A. dubius</i>	offshore deeper waters	North Carolina to Greenland		68-76 70.8	56-67 61.8	28-35 31.1	124- 147 132.1	Nizinski et al. 1990
<i>A. dubius</i>	coastal	Newfoundland	Late Fall to early Spring	70-77 73.8	60-68	30-36		Winters & Dalley 1988
<i>A. dubius</i>	offshore	W Greenland to Georges Bank		70-78				Winters & Dalley 1988
<i>A. dubius</i>	inshore	W Greenland to Gulf of Maine		70-78				Winters & Dalley 1988

Table 2 (continued): Synopsis of Data on North Atlantic Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert.	Dorsal	Anal	Plicae	
<i>A. marinus</i>	inshore offshore	Faroes to St. Kilda Shetland to Firth of Forth	Early Spring	67-72 69.2	56-62 59.07	28-33 30.6		Raitt 1934
<i>A. marinus</i>		Celtic Sea		67-70				Corbin & Vati 1949
<i>A. marinus</i>		Baltic Sea		65-72				Kändler 1941
<i>A. marinus</i>	offshore deeper water	Helgoland		Avg. 69.9				Kändler 1936- 1937
<i>A. marinus</i>		Faroes		68-72				Bruun 1941
<i>A. marinus</i>		Iceland		68-73				Bruun 1941
<i>A. marinus</i>	larvae off all coasts	Iceland	Spring	69-75				Einarsson 1951
<i>A. marinus</i>	fiords & coastal	W. Greenland 72°20'N- 60°30'N	Winter	67-72 69.39	55-62 59.05	28-32 30.27		Jensen 1941
<i>A. marinus</i>		S Norway Bergen		67-72				Soleim 1945

Table 2 (continued): Synopsis of Data on North Atlantic Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert.	Dorsal	Anal	Plicae	
<i>A. marinus</i>		N Norway Grense, Jakobselv		69-75				Soleim 1945
<i>A. marinus</i>		Tana		69-74				Soleim 1945
<i>A. marinus</i>		Iceland	spring	71.1				Kändler 1936, 1937
<i>A. marinus</i>		Iceland		69-73				Kändler 1941
<i>A. tobianus</i>	inshore	Europe		63	54-59	27-30	120-130	Günther 1862
<i>A. tobianus</i> (= <i>A. lancea</i>)	inshore	Scotland to Faroës	Summer	60-66 63.4	51-56 53.4	26-31 27.96		Raitt 1934
<i>A. tobianus</i>		Exmouth		62-66				Corbin and Vati 1949
<i>A. tobianus</i> (= <i>A. lancea</i>)	Shallow waters fiords & coast	Danish waters		61-65 63.3	51-56 53.4	26-31 28.2		Jensen 1941
<i>A. tobianus</i> (= <i>A. lancea</i>)	shallow coastal	Cuxhaven	Spring	61-65 63.1	53.4	28.1		Kändler 1936-37
<i>A. tobianus</i> (= <i>A. lancea</i>)	inshore	Helgoland Island	Summer	64.1	54.2	27.7		Kändler 1936-37

Table 2 (continued): Synopsis of Data on North Atlantic Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert.	Dorsal	Anal	Plicae	
<i>A. tobianus</i>		North Sea & Baltic	Autumn	60-68				Kändler 1941
<i>A. tobianus</i>	post larvae coastal	S & W coast Iceland	Spring	60-65				Einarsson 1951
<i>A. tobianus</i> (= <i>A. lancea</i>)		Iceland		60-65 62.6	51-54 52.9	26-28 27.1		Bruun 1941
<i>A.</i> <i>tobianus</i> (= <i>A. lancea</i>)		Faroes		63-66 64.5	53-57 54.7	27-30 28.5		Bruun 1941
<i>A. tobianus</i>		Soviet northern seas		< 66	< 57			Andriyashev 1954
<i>A. t.</i> <i>oceanicus</i>	offshore	S of Cape Cod		67-72	56-64	27-33		Perlmutter 1940
<i>A. hexapterus</i>		Soviet Northern seas		> 66	> 57			Andriyashev 1954
<i>A. hexapterus</i>		Kuriles Islands		70		30		Pallus 1831
<i>A. hexapterus</i>		circumpolar		66-74	57-65	28-36		Walters 1955

Table 2 (continued): Synopsis of Data on North Atlantic Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert.	Dorsal	Anal	Plicae	
A <i>hexapterus</i> Syn. A. <i>americanus</i>	circum- polar inshore	41-60°N NW Atlantic		61-73	51-62	23-32		Richards et al. 1963
A. <i>americanus</i>	inshore	New York			56,60			Dekay 1842
A. <i>americanus</i>					54-60	28-31	130	Günther 1862
A. <i>americanus</i>		Labrador		64-69	57-60	28-31		Backus 1957
A. <i>americanus</i>	shallow coastal waters	Labrador to southern Delaware		62-70 66.4	52-61 57.4	26-33 29.4	106-126 117.4	Nizinski et al. 1990

Table 3: Synopsis of Data on North Pacific Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert	Dorsal	Anal	Plicae	
<i>A. personatus</i>					55	25		Günther 1862
<i>A. personatus</i>		Port Clarence Alaska			53-61	26-30	135- 147	Scofield, 1899
<i>A. personatus</i>		Puget Sound			57-59	28-31	133- 151	Scofield, 1899
<i>A. personatus</i>		Bering Island			60-64	30-31	146- 159	Jordan & Gilbert, 1899
<i>A. personatus</i>		Makushin Bay Unalaska			61-63	30-32	145- 159	Jordan & Gilbert, 1899
<i>A. personatus</i>		Unalaska					183	Jordan & Gilbert, 1899
<i>A. personatus</i>		Puget Sound			58-59	29-31	136, 144- 158	Jordan & Gilbert, 1899
<i>A. personatus</i>	inshore	Amiji Isl. Japan		60-66				Okamoto <i>et</i> <i>al.</i> 1988

Table 3 (continued): Synopsis of Data on North Pacific Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert	Dorsal	Anal	Plicae	
<i>A. personatus</i>	coastal	Rishiri Is.		mean 65.41	mean 56.72	mean 30.94		Kitaguchi 1978
<i>A. personatus</i>	coastal	Shakotan Pen.		mean 65.67	mean 57.13	mean 31.16		Kitaguchi 1978
<i>A. personatus</i>	coastal	E. of Cape Soya		mean 65.75	mean 56.64	mean 30.75		Kitaguchi 1978
<i>A. personatus</i>	inshore	southern seas including Sendai Bay and western seas from Torrori Pref.		63	55 or 56	30 or 31		Hashimoto 1991
<i>A. hexapterus</i>	inshore	Cape Soya NE Hokkaido		65-70				Okamoto 1989
<i>A. hexapterus</i>		Gulf of Anadyr		67-70	55-60	28-32		Andriyashev 1954

Table 3 (continued): Synopsis of Data on North Pacific Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert	Dorsal	Anal	Plicae	
<i>A. personatus</i>	inshore	Cape Soya NE Hokkaido		64-68				Okamoto 1989
<i>A. personatus</i>				60-66	51-56		150- 160	Hashimoto & Kawasaki 1981
<i>A. personatus</i>	inshore	Japan N&S		59-69	53-59	27-33		Hatanaka & Okamoto 1950
<i>A. personatus</i>	inshore	Near Oshika Peninsula & Kinkasan, Central Sendai Bay	Late Dec. to Jan.	60-66		20-28		Hatanaka & Okamoto 1950
<i>A. personatus</i>	coastal	Kinkasan, Terama	late Dec.	59-66, Mode 62				Hatanaka & Okamoto 1950
<i>A. personatus</i>	coastal	Kinkasan, On Board	late Jan.	60-64, Mode 62				Hatanaka & Okamoto 1950
<i>A. personatus</i>	coastal	Kinkasan, Onagawa	Mid Jan to May	59-67, Mode 62				Hatanaka & Okamoto 1950

Table 3 (continued): Synopsis of Data on North Pacific Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert	Dorsal	Anal	Plicae	
<i>A. personatus</i>	coastal	Kinkasan, Off Yuriage	Aug. & Nov.	60-65, Mode 62				Hatanaka & Okamoto 1950
<i>A. personatus</i>	coastal	Kinkasan, Takenoura	Mid March	61-67, Mode 62				Hatanaka & Okamoto 1950
<i>A. personatus</i>	coastal	Hokkaido, Off Yoichi	May & June	60-67, Mode 64				Hatanaka & Okamoto 1950
<i>A. personatus</i>	coastal	Ise Bay	Late Jan. - May	59-64, Mode 62				Hatanaka & Okamoto 1950
<i>A. personatus</i>	coastal	North, South, East Kokkaido		61-69 mode mostly 65 N-S cline		29-34 mode most 31		Ishigaki & Kaga 1957
<i>A. personatus</i>	coastal	Wakkanai		mean 65.26				Kitaguchi 1978
<i>A. personatus</i>	coastal	Yagishiri Is.		mean 65.53				Kitaguchi 1978

Table 3 (continued): Synopsis of Data on North Pacific Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert	Dorsal	Anal	Plicae	
<i>A. hexapterus</i>		Sea of Okhotsk		67-70	57-60		145- 164	Lindberg 1937
<i>A. hexapterus</i>				67-72	56-64			Lindberg 1937
<i>A. hexapterus</i>	inshore	Wakkanai		65-70	55-59	28-32		Hashimoto 1984
<i>A. hexapterus</i>	coastal	Wakkanai (July)		67	57	30		Hashimoto 1991
<i>A. hexapterus</i>	coastal	E. of Cape Soya		mean 67.73	mean 56.73	mean 29.67		Kitaguchi 1978
<i>A. hexapterus</i>	inshore offshore	Okhotsk Sea 45°-50°N	June- August	64-70 (67.6)				Kobayashi 1961
<i>A. hexapterus</i>	inshore offshore	Okhotsk Sea 50°-55°N	July- August	65-73 (68.6)				Kobayashi 1961
<i>A. hexapterus</i>	inshore offshore	Bering Sea 50°-55°N	June- August	65-74 (68.6)				Kabayashi 1961
<i>A. hexapterus</i>	inshore offshore	Bering Sea 60°-65°N	August	65-73 (70.0)				Kabayashi 1961

Table 3 (continued): Synopsis of Data on North Pacific Species of *Ammodytes*

Species Subspecies	Habitat	Location	Spawning Time	Meristics				Author Date
				Vert	Dorsal	Anal	Plicae	
<i>A. hexapterus</i>	inshore offshore	Bering Sea 55°-60°N	July	64-73 (68.23)				Kabayashi 1961
<i>A. japonicus</i>		Hokkaido			51-59	26-33	165- 188	Duncker and Mohr 1940
<i>A. t. japonicus</i>		Pacific		64-68	55-59	28-32		Perlmutter 1940
<i>A. t. minami</i>		Pacific		62-64	52-56	26-30		Perlmutter 1940
<i>A. aleutensis</i>		Pacific			54-62	28-32	147- 169	Duncker and Mohr 1940
<i>A. personatus</i>	inshore	Hokkaido to Sendai Bay; off Tottori Perf.		65 or 66	57 or 58	31 or 32		Hashimoto 1991
<i>A. personatus</i>	coastal	N. of Cape Soya		mean 65.84	mean 56.6	mean 30.64		Kitaguchi 1978
<i>A. personatus</i>	coastal	Esashi		mean 65.51				Kitaguchi 1978

Table 4: Data set for transformation series hypothesis (2)

Trichonotidae	02100	00100	00000	00010	01100	00110	01001	00001	00000
Trachinidae	00001	20000	00100	00000	01000	?0010	01110	11000	10000
Uranoscopidae	00000	20000	00100	00100	10000	??110	01101	11000	10000
<i>E. mitsukurii</i>	02110	00001	11001	00021	11100	00110	11111	10011	10000
<i>E. sarisa</i>	01000	00001	1100?	?0???	??10?	?0?1?	?1111	10011	10001
<i>B. viridianguilla</i>	02110	00011	11001	?0021	1110?	?0?1?	?1111	10011	10000
<i>B. renniei</i>	02101	12011	11002	?0???	??10?	?1?1?	?1111	10011	10011
<i>B. gilli</i>	02102	12011	11002	?0???	??10?	?1?1?	?1111	10011	10011
<i>A. tobianus</i>	12112	21211	11113	10110	00100	11111	11111	10111	10011
<i>A. americanus</i>	12112	21311	11113	11111	01100	11111	11111	10111	11111
<i>A. dubius</i>	12112	21311	11113	11121	01100	11111	11111	10111	11111
<i>A. marinus</i>	12113	21211	11113	11121	01100	11111	11111	10111	11111
<i>A. hexapterus</i>	12113	21211	11113	11121	01100	11111	11111	10111	11111
<i>A. personatus</i>	12113	21211	11113	111??	??100	11111	11111	10111	11111
<i>H. immaculatus</i>	12111	21211	11113	11110	0?111	11111	11111	10111	11111
<i>H. lanceolatus</i>	12111	21211	11113	11110	0?111	11111	11111	10111	11111
<i>G. semisquamatus</i>	12111	21211	11224	11010	11100	12111	11111	10111	11111
<i>G. cicereus</i>	12111	21211	11214	10???	??100	12111	11111	10111	11111
<i>G. capensis</i>	12111	21211	11224	?1???	??100	12111	11111	10111	11111

Table 5: Data set for transformation series hypothesis (4)

Trichonotidae	02100	00100	00000	00	00010	01100	00110	01001	00001	00000
Trachinidae	00001	20000	00100	00	00000	01000	?0010	01110	11000	10000
Uranoscopidae	00000	20000	00100	00	00100	10000	??110	01101	11000	10000
<i>E. mitsukurii</i>	02110	00001	11001	00	00021	11100	00110	11111	10011	10000
<i>E. sarisa</i>	01000	00001	1100?	??	?0???	??10?	?0?1?	?1111	10011	10001
<i>B. viridianguilla</i>	02101	00011	11001	00	?0021	1110?	?0?1?	?1111	10011	10000
<i>B. renniei</i>	02102	12011	11002	00	?0???	??10?	?1?1?	?1111	10011	10011
<i>B. gilli</i>	02112	12011	11002	00	?0???	??10?	?1?1?	?1111	10011	10011
<i>A. tobianus</i>	12112	21211	11112	10	10110	00100	11111	11111	10111	10011
<i>A. americanus</i>	12112	21311	11112	10	11111	01100	11111	11111	10111	11111
<i>A. dubius</i>	12112	21311	11112	10	11121	01100	11111	11111	10111	11111
<i>A. marinus</i>	12113	21211	11112	10	11121	01100	11111	11111	10111	11111
<i>A. hexapterus</i>	12113	21211	11112	10	11121	01100	11111	11111	10111	11111
<i>A. personatus</i>	12113	21211	11112	10	111??	??100	11111	11111	10111	11111
<i>H. immaculatus</i>	12111	21211	11112	10	11110	0?111	11111	11111	10111	11111
<i>H. lanceolatus</i>	12111	21211	11112	10	11110	0?111	11111	11111	10111	11111
<i>G. semisquamatus</i>	12111	21211	11222	01	11010	11100	12111	11111	10111	11111
<i>G. cicereus</i>	12111	21211	11212	01	10???	??100	12111	11111	10111	11111
<i>G. capensis</i>	12111	21211	11222	01	?1???	??100	12111	11111	10111	11111

Table 6: Data set for transformation series hypothesis (5)

Trichonotidae	02100	00100	00000	00	00010	01100	00110	01001	00001	00000
Trachinidae	00001	20000	00100	00	00000	01000	?0010	01110	11000	10000
Uranoscopidae	00000	20000	00100	00	00100	10000	??110	01101	11000	10000
<i>E. mitsukurii</i>	02110	00001	11001	00	00021	11100	00110	11111	10011	10000
<i>E. sarisa</i>	01000	00001	1100?	??	?0???	??10?	?0?1?	?1111	10011	10001
<i>B. viridiangui</i>	02110	00011	11001	00	?0021	1110?	?0?1?	?1111	10011	10000
<i>B. renniei</i>	02101	12011	11001	02	?0???	??10?	?1?1?	?1111	10011	10011
<i>B. gilli</i>	02102	12011	11001	02	?0???	??10?	?1?1?	?1111	10011	10011
<i>A. tobianus</i>	12112	21211	11111	10	10110	00100	11111	11111	10111	10011
<i>A. americanus</i>	12112	21311	11111	10	11111	01100	11111	11111	10111	11111
<i>A. dubius</i>	12112	21311	11111	10	11121	01100	11111	11111	10111	11111
<i>A. marinus</i>	12113	21211	11111	10	11121	01100	11111	11111	10111	11111
<i>A. hexapterus</i>	12113	21211	11111	10	11121	01100	11111	11111	10111	11111
<i>A. personatus</i>	12113	21211	11111	10	111??	??100	11111	11111	10111	11111
<i>H. immaculatus</i>	12111	21211	11111	10	11110	0?111	11111	11111	10111	11111
<i>H. lanceolatus</i>	12111	21211	11111	10	11110	0?111	11111	11111	10111	11111
<i>G. semisquamatus</i>	12111	21211	11221	01	11010	1?100	12111	11111	10111	11111
<i>G. cicereus</i>	12111	21211	11211	01	10???	??100	12111	11111	10111	11111
<i>G. capensis</i>	12111	21211	11221	01	?1???	??100	12111	11111	10111	11111

Table 7: Data set from Pietsch and Zebatian (1990) with ammodytid genera added, new characters and revised coding

Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	000
Cheimarrichthyidae	11000	00000	00000	00000	00000	00000	00000	00000	000
Pinguipedidae	11100	00000	00000	00000	00000	00000	00000	00000	000
Percophidae	11171	00000	00000	00000	00000	00001	10000	00000	000
Trichonotidae	11030	00000	00000	01100	00100	00001	10101	11000	000
Creediidae	11040	00000	00000	00000	00000	00001	10000	00000	000
Champsodontidae	01161	1?000	00000	00000	00000	00000	00000	00000	000
Chiasmodontidae	01050	11000	00000	00000	00000	00000	00000	00000	000
Leptoscopidae	11141	01111	11111	10000	00000	00000	00100	00000	000
<i>Embolichthys</i>	00131	00000	00000	01110	11101	10000	01001	11111	100
<i>Bleekeria</i>	0?131	00000	00001	01110	11101	10000	01011	11111	100
<i>Hyperoplus</i>	0?131	00010	00001	01111	11101	10000	01211	11111	111
<i>Ammodytes</i>	0?131	00010	00001	01111	11101	10000	01211	11111	111
<i>Gymnammodytes</i>	0?131	00000	00001	01110	11101	10000	01211	11111	111
Trachinidae	11111	11110	00000	01111	11111	11110	00000	00000	000
Uranoscopidae	11121	11111	11111	11111	10111	11110	00000	10000	000

Table 8: Tree statistics from transformation series hypotheses

Hypothesis	Tree Statistics			Consensus			Optimization		
	# trees	l	ci	ri	l	ci	ri	l	T S
1	9	76	75	89	77	74	88	77	5
2	3	75	76	89	76	75	88	76	4
3	3	76	75	88	77	74	87	77	5
4	3	76	75	88	77	74	87	77	5
5	3	77	74	87	78	73	87	78	6
3-Taxon	3	78	73	87	78	73	87	78	4

Column legends: Hypothesis = particular transformation series hypothesis referred to in text or trees generated by the 3-taxon transformation program TAX (3-Taxon), # trees = number of trees generated by data set representing a particular transformation series hypothesis for labial ossicles (Character 15), l = length of tree, ci = consistency index, ri = retention index, TS = Number of steps with either character 15 or characters 15, 16 and 17, depending on appropriate hypothesis (see text for details), optimized onto tree. The tree statistics for the 3-Taxon transformation trees were calculated with the data sets for hypothesis 2 optimized on the trees. The optimization of the 3-taxon has character (15) of hypothesis 2 mapped on the 3-taxon transformation consensus tree (Figure 140).

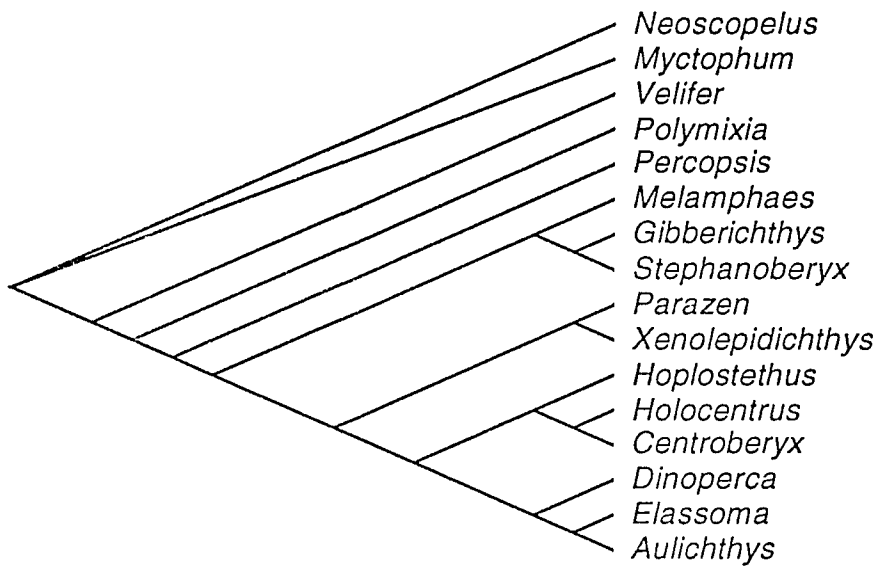


Figure 1a

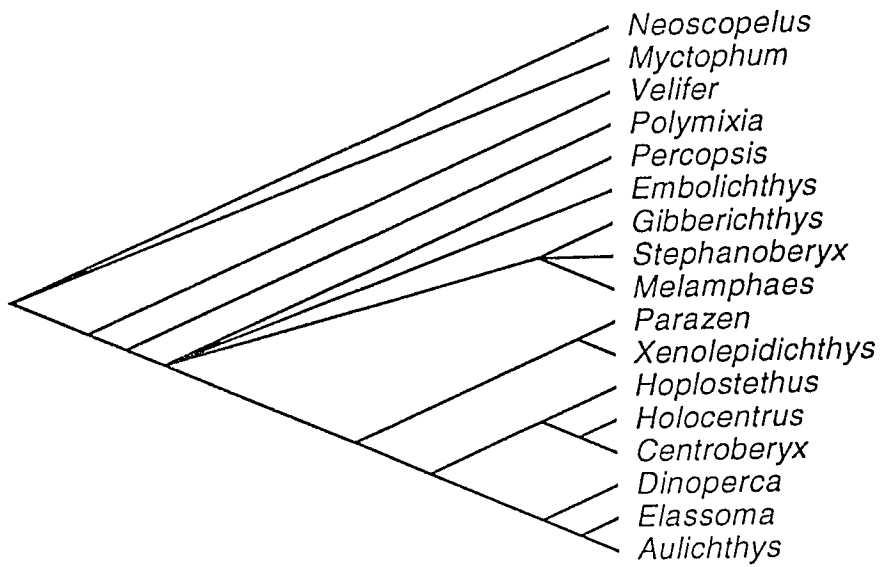


Figure 1b

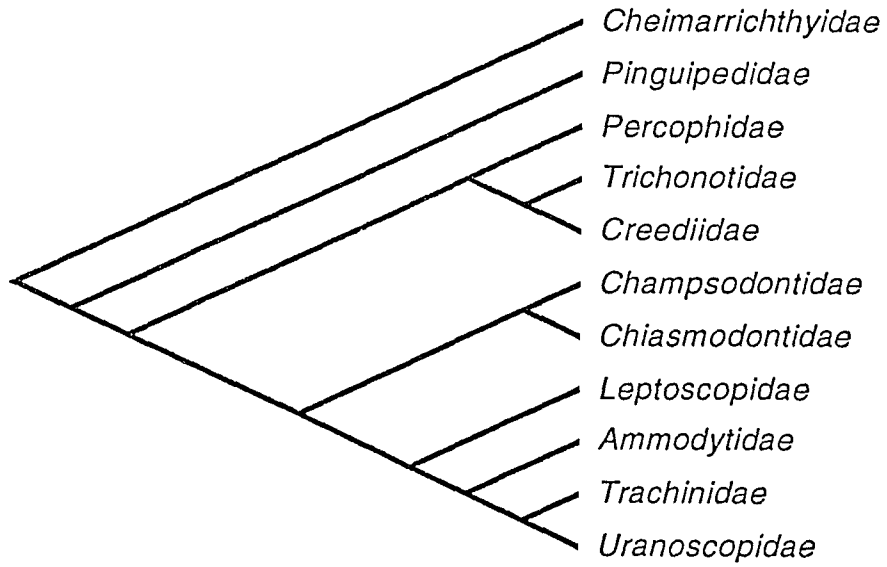


Figure 2a

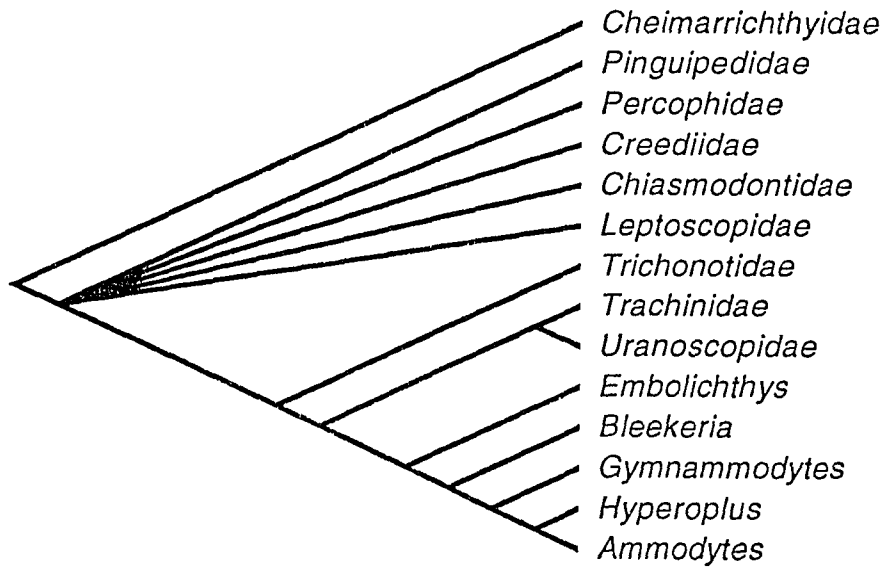


Figure 2b

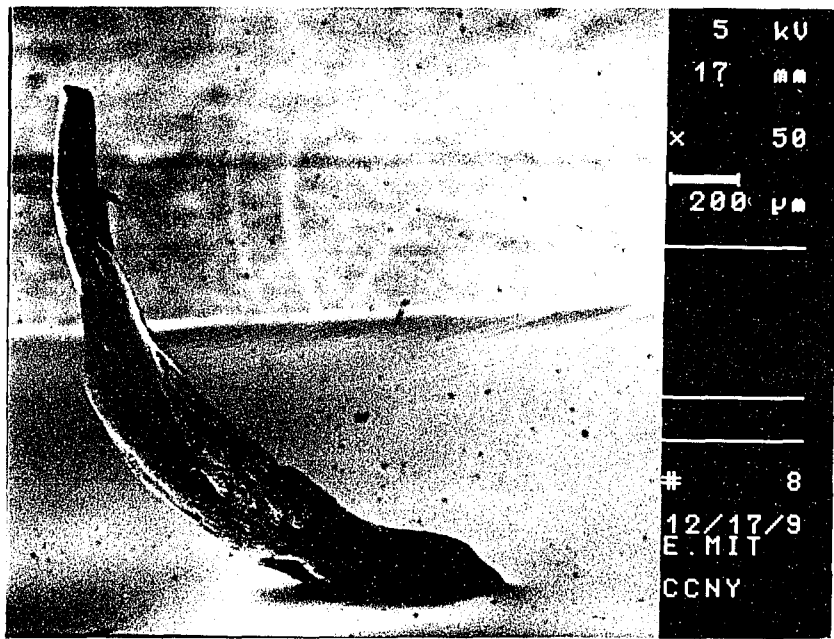


Figure 3a

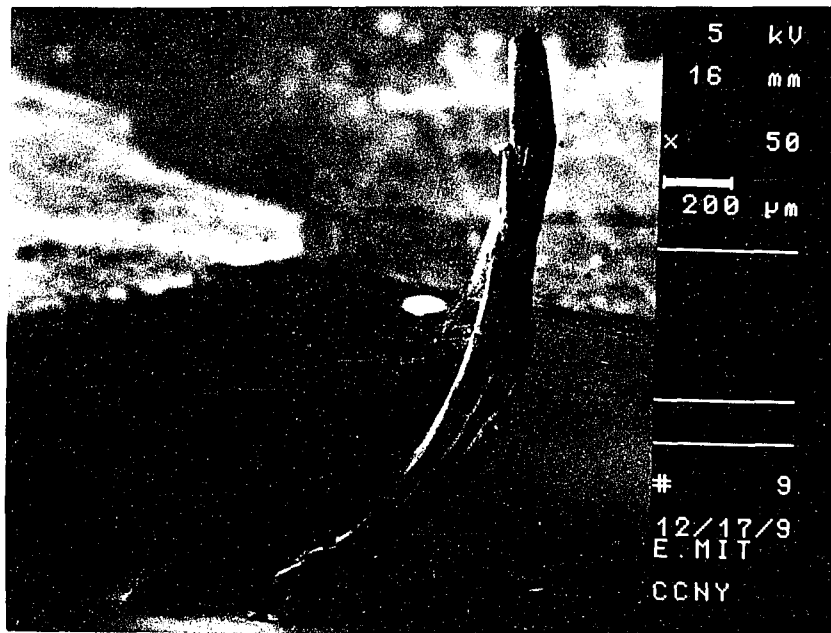


Figure 3b

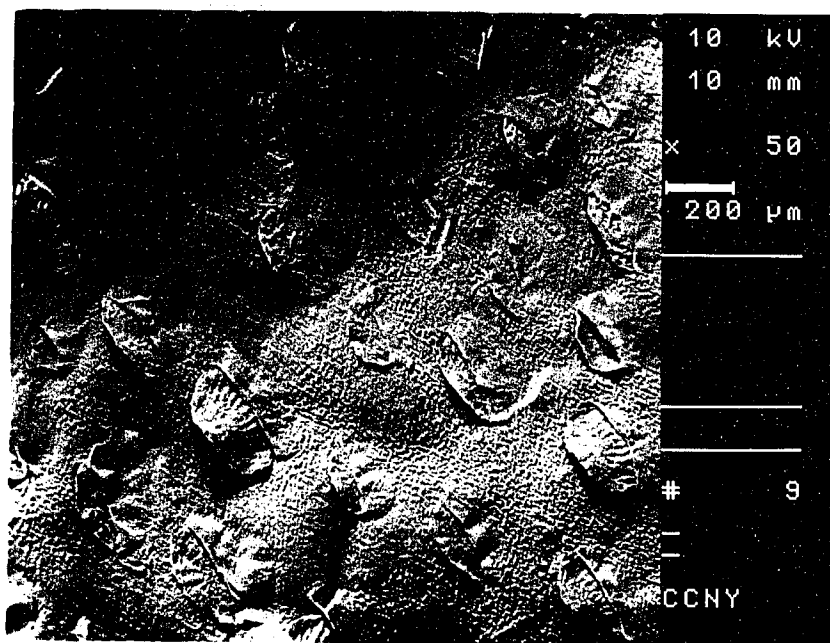


Figure 4a

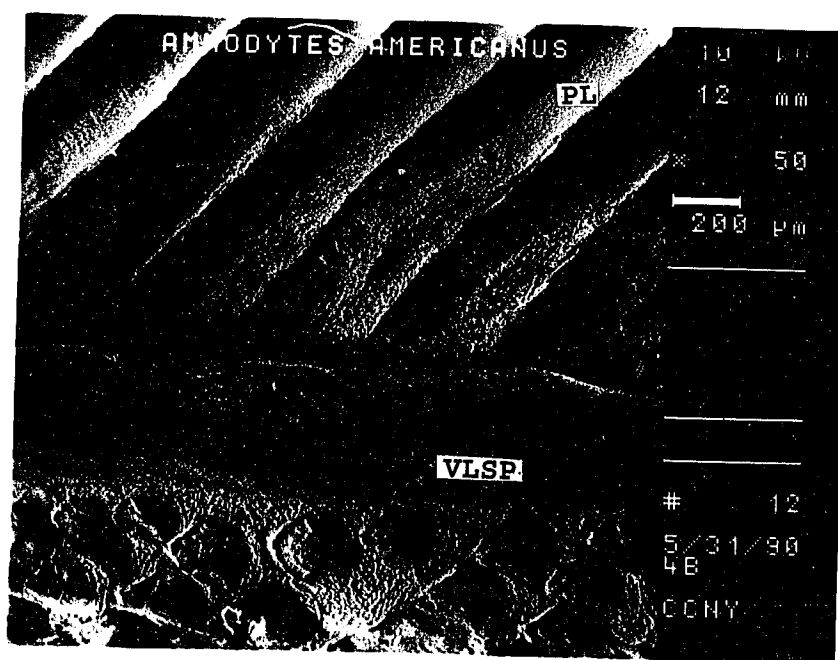


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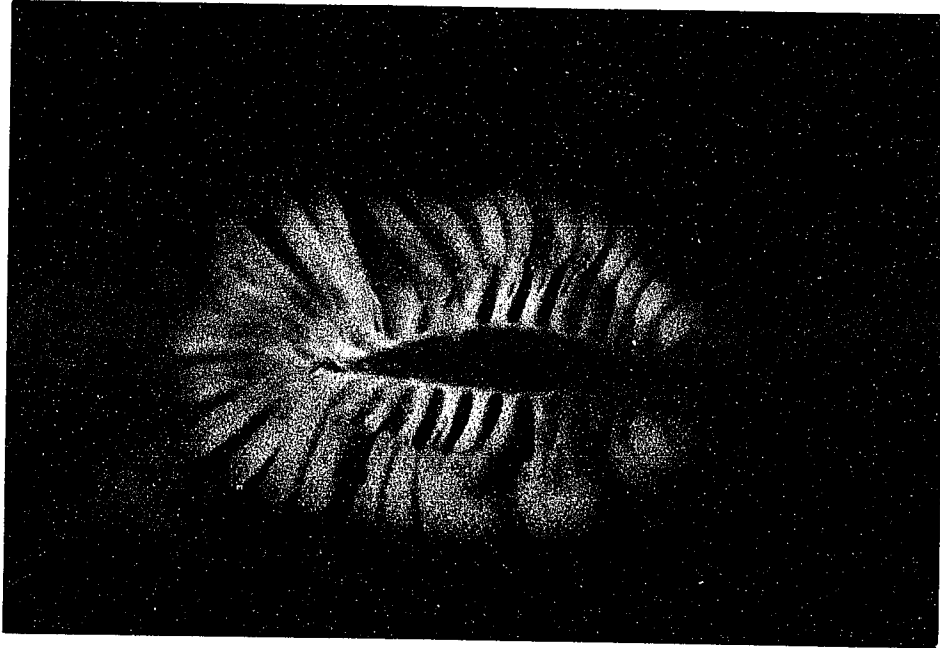


Figure 5



Figure 6

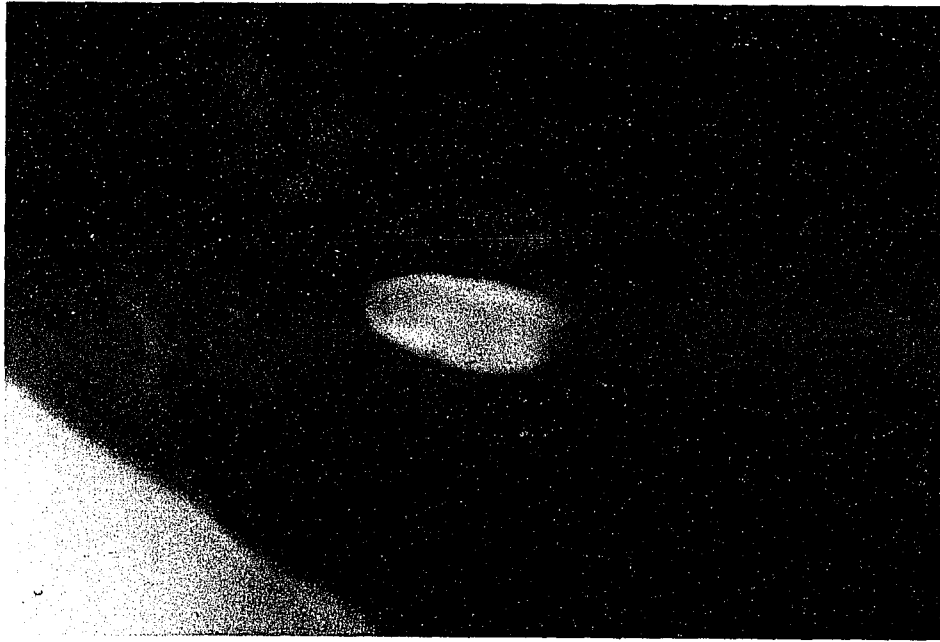


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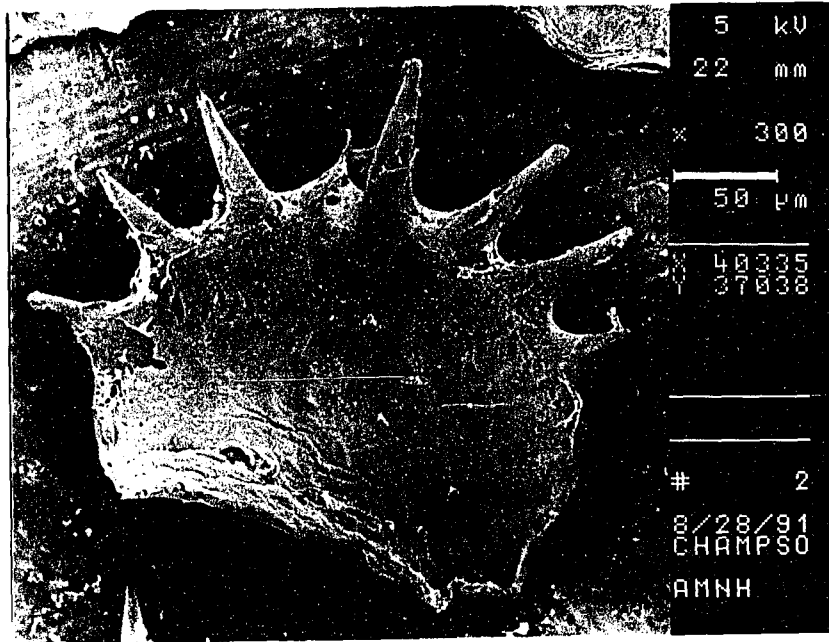


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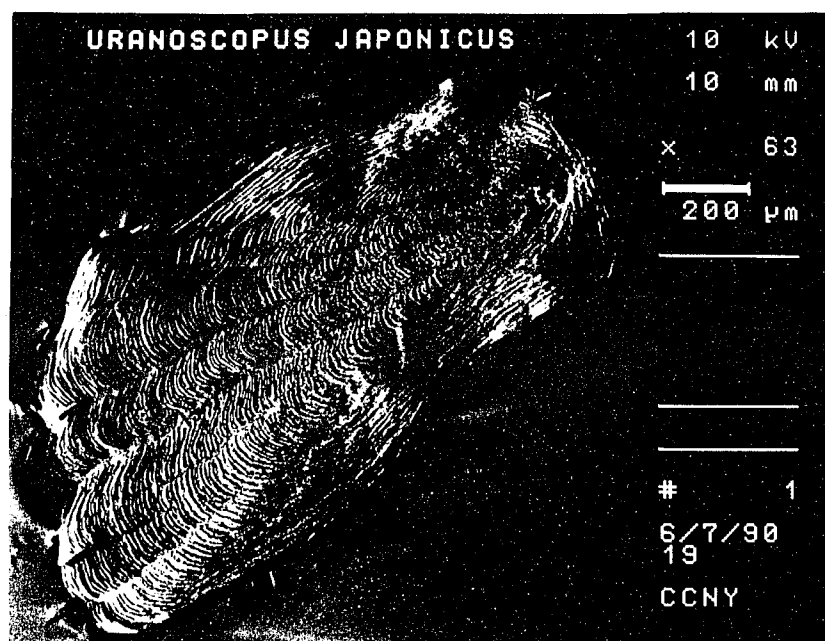


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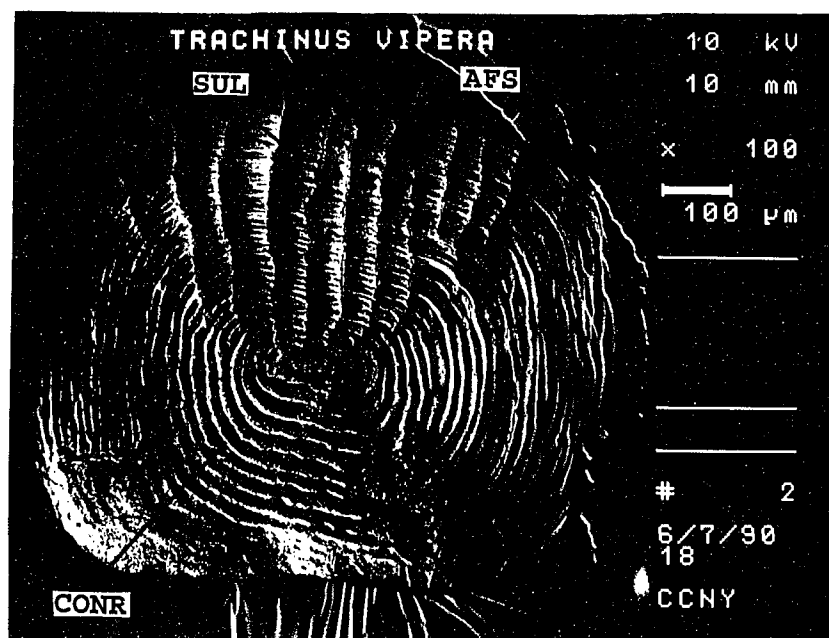


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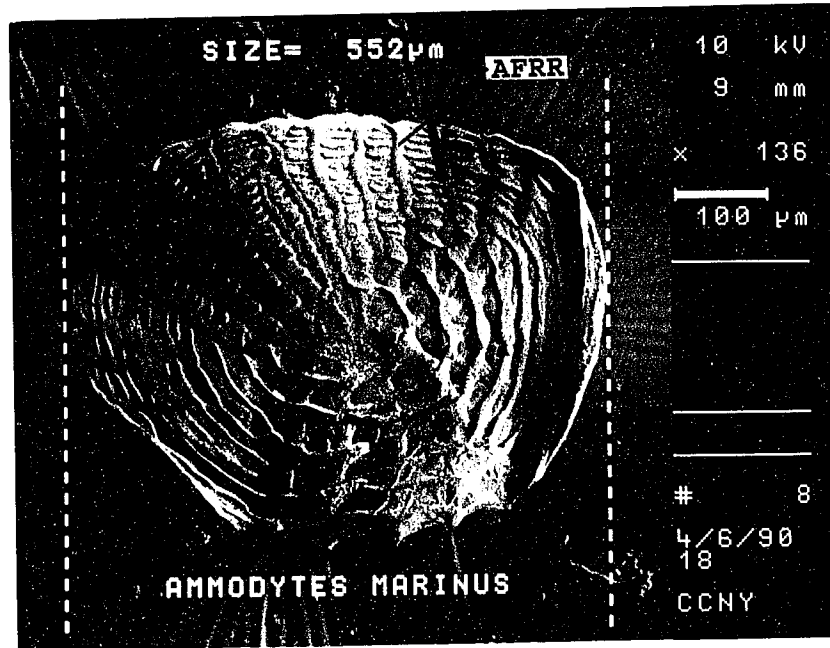


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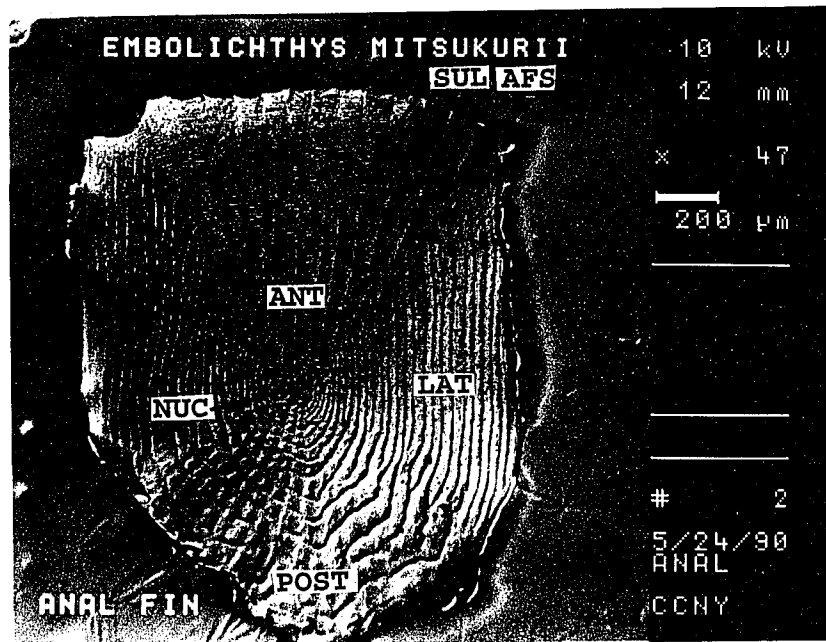


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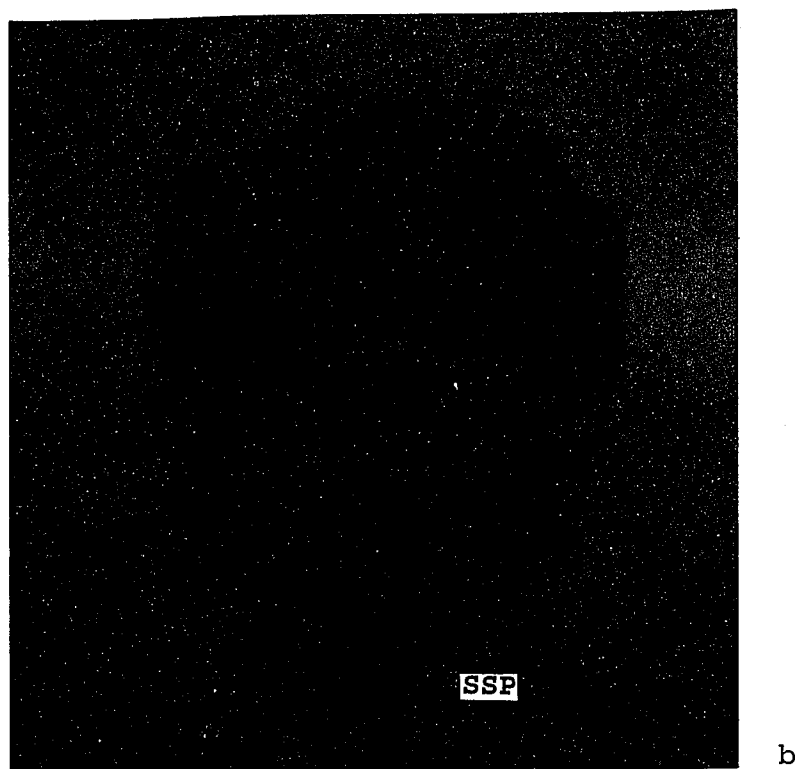
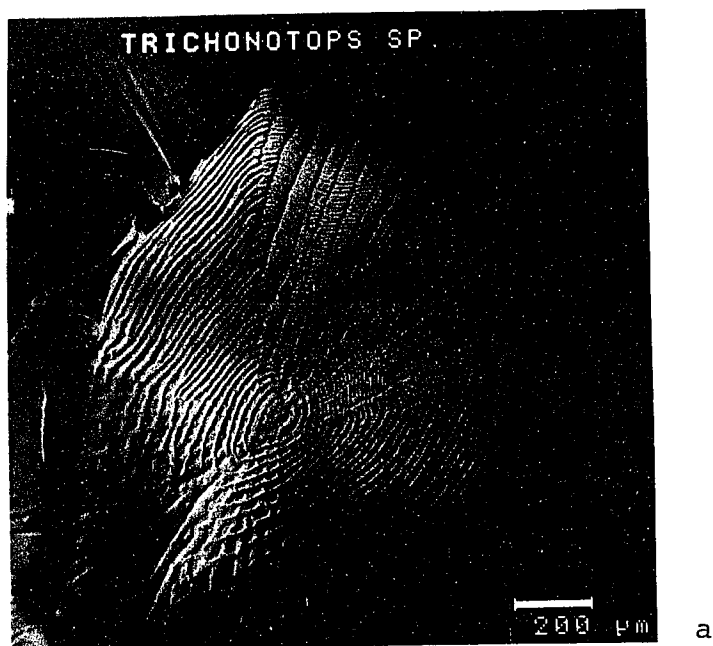


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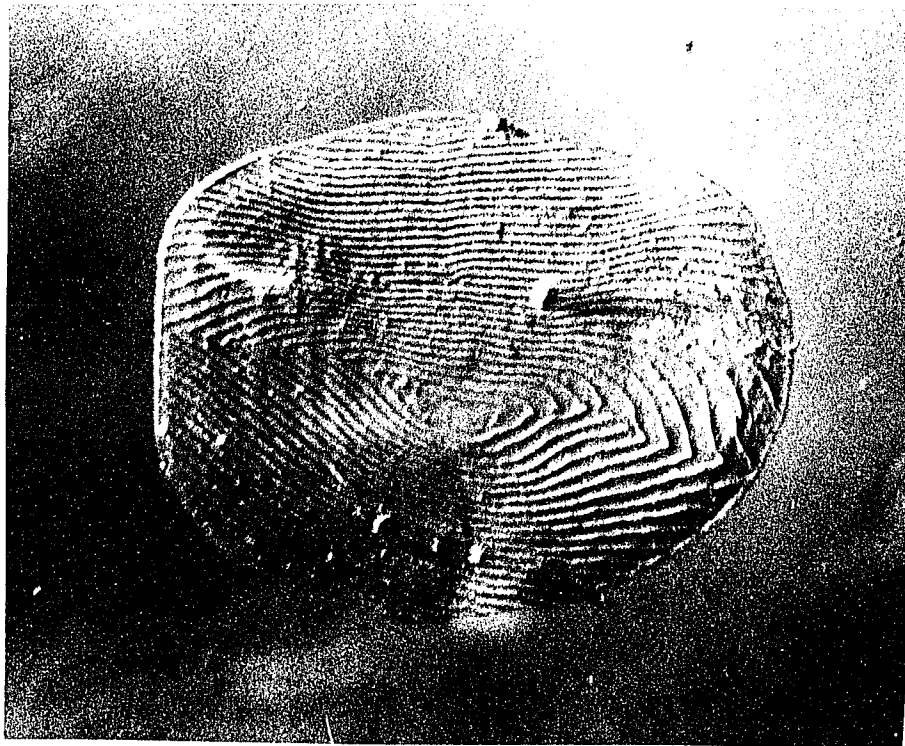


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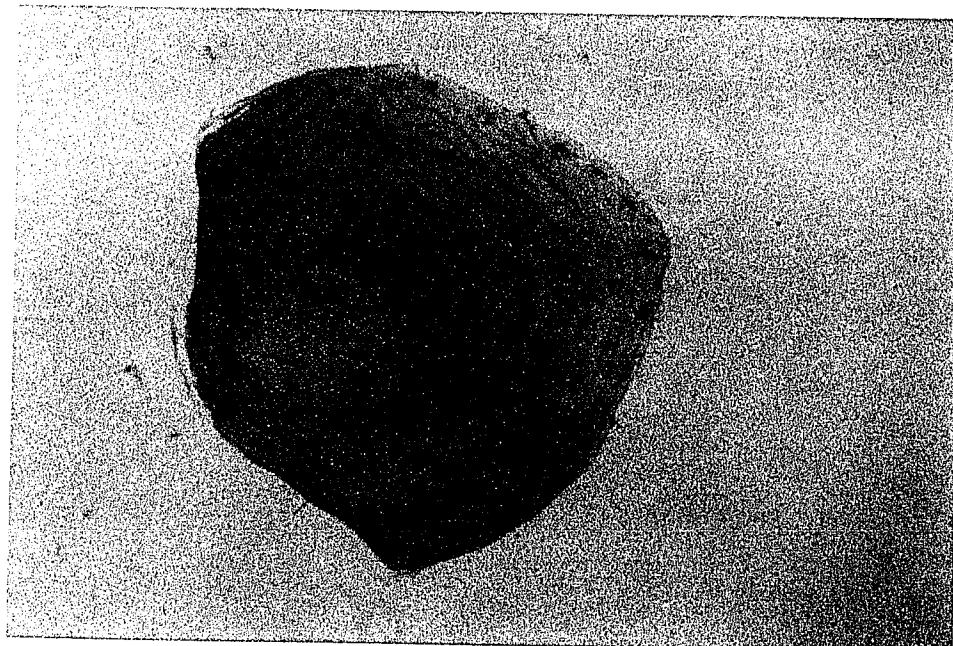


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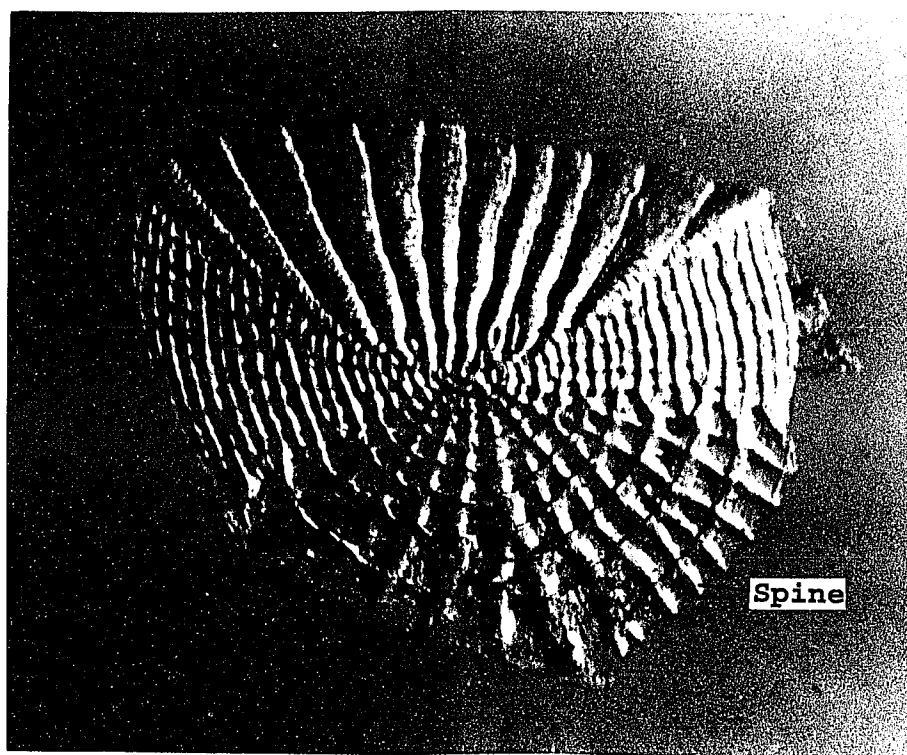


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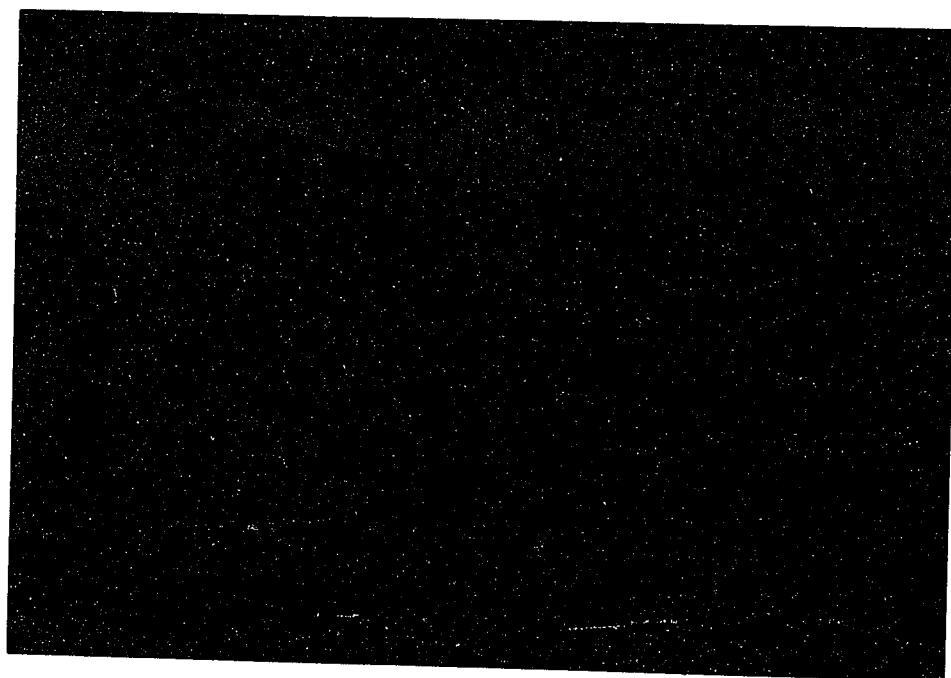
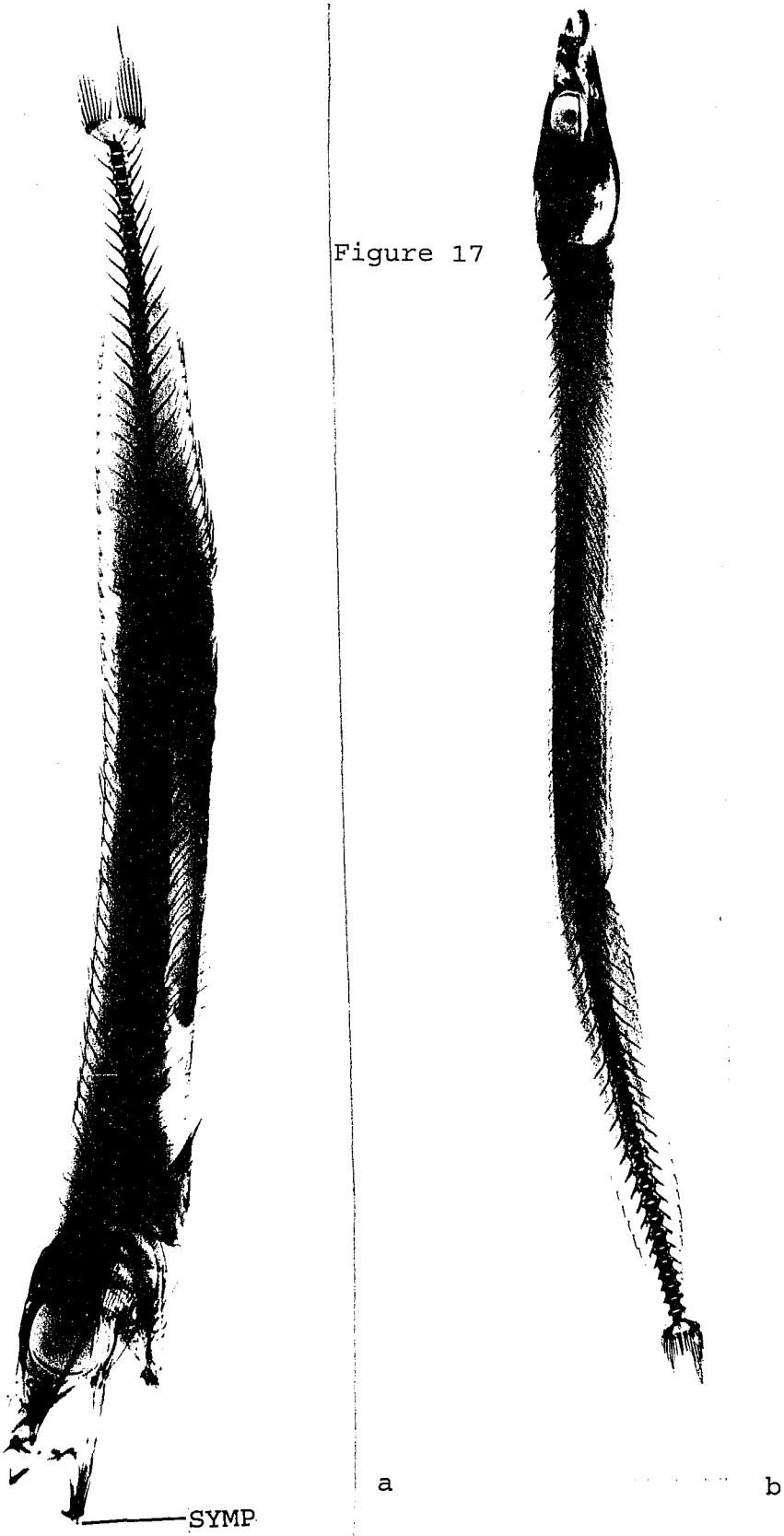


Figure 18

Figure 17



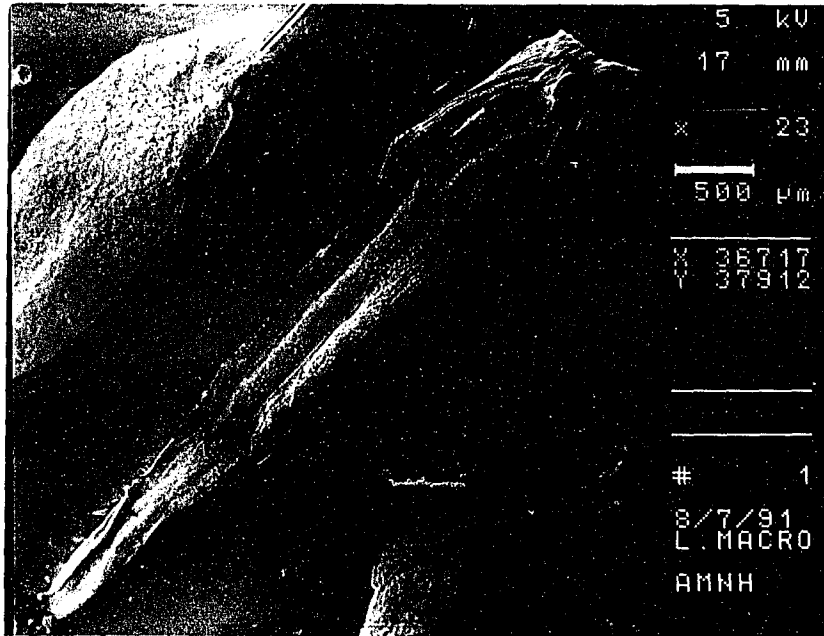


Figure 19



Figure 20



Figure 21

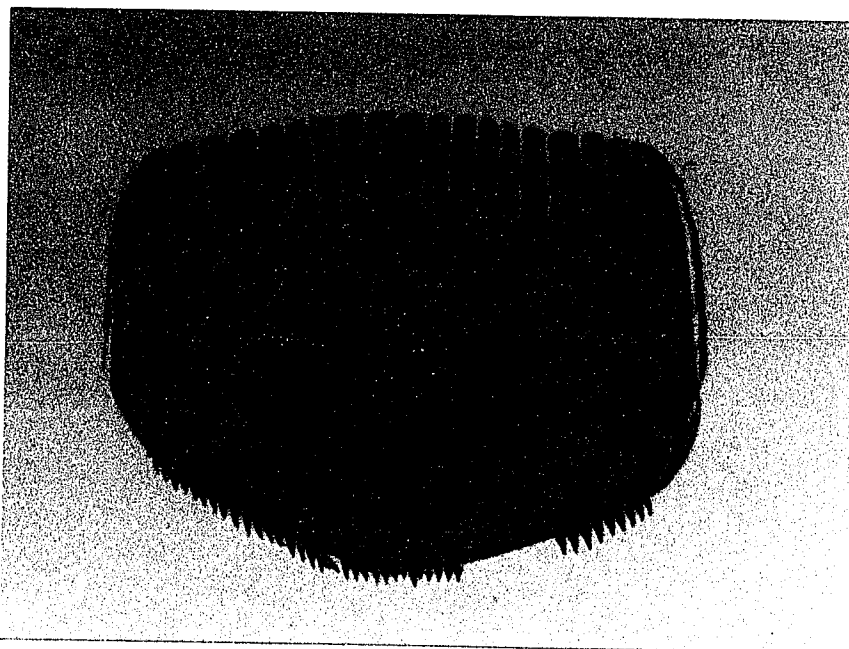


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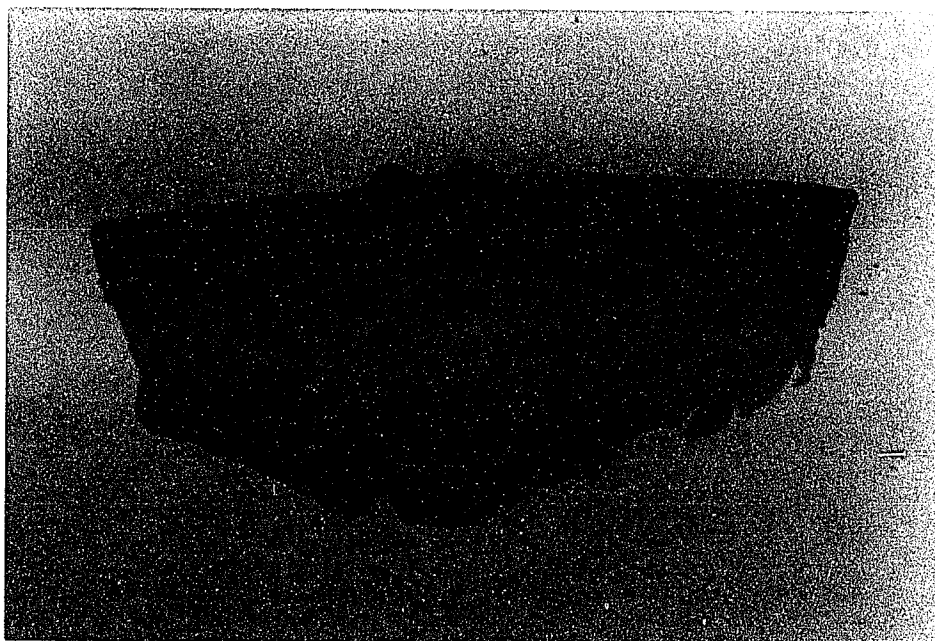


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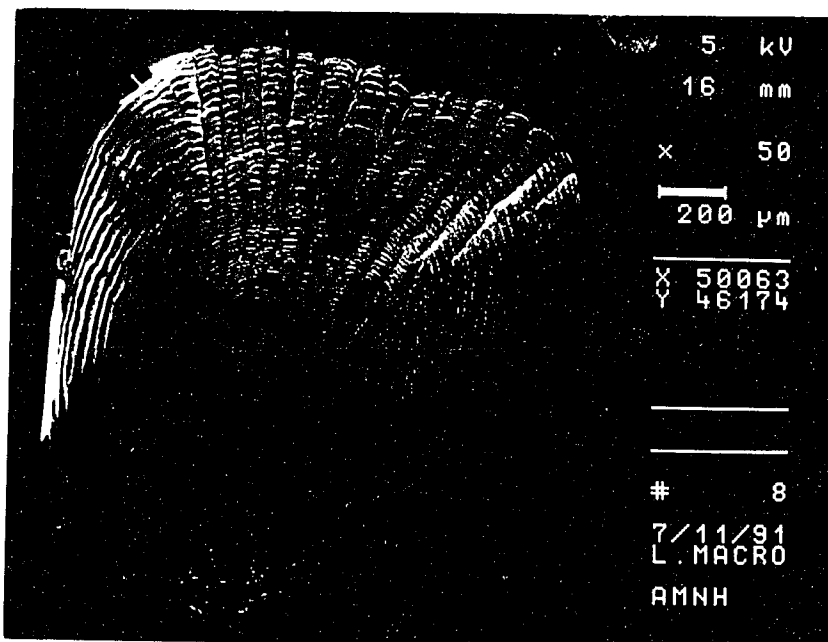


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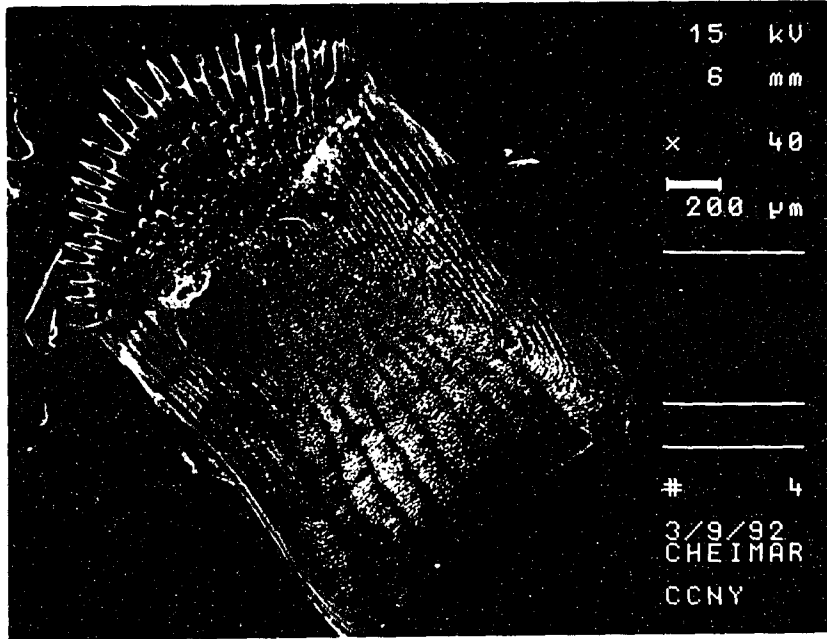


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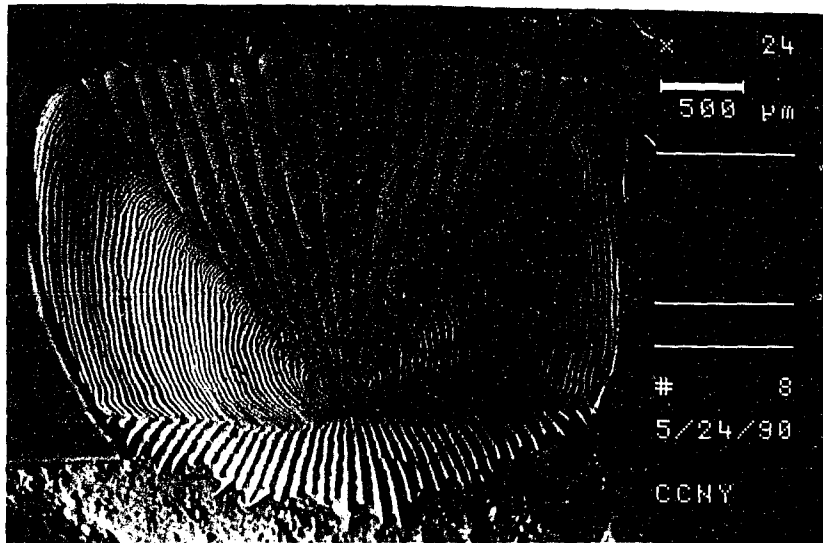


Figure 26



Figure 27



Figure 28

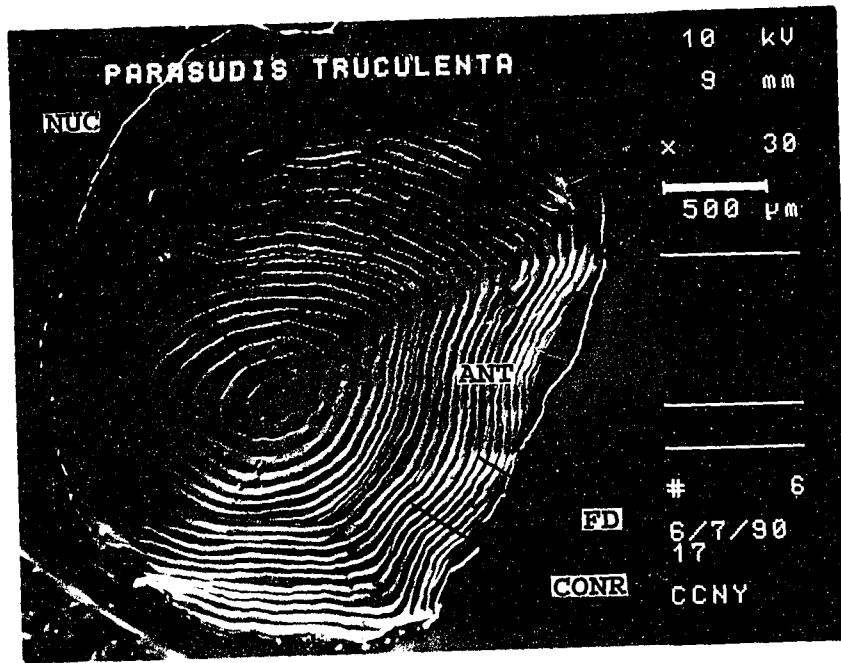


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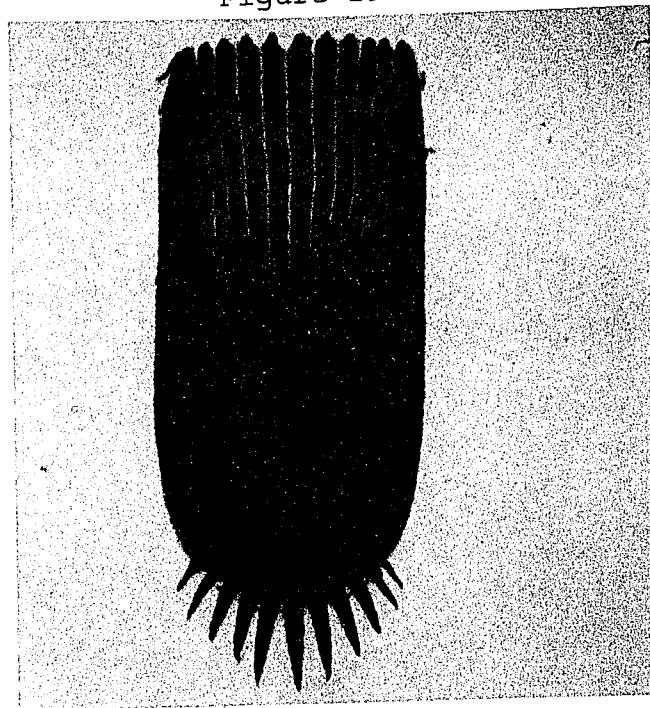


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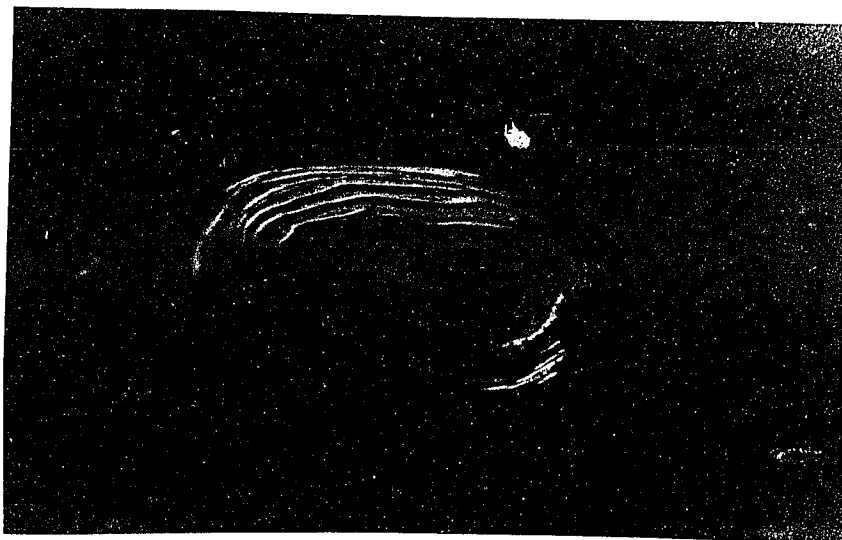


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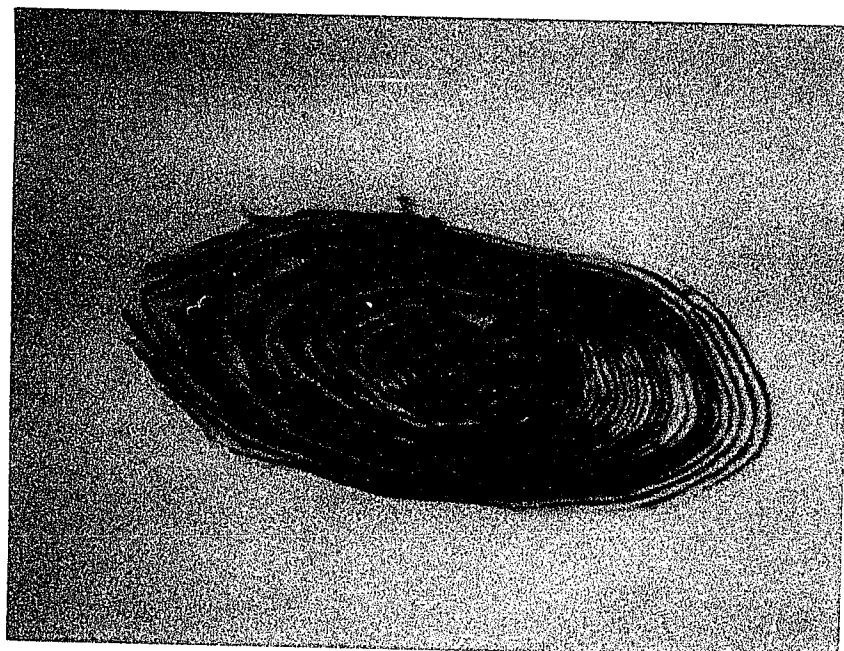


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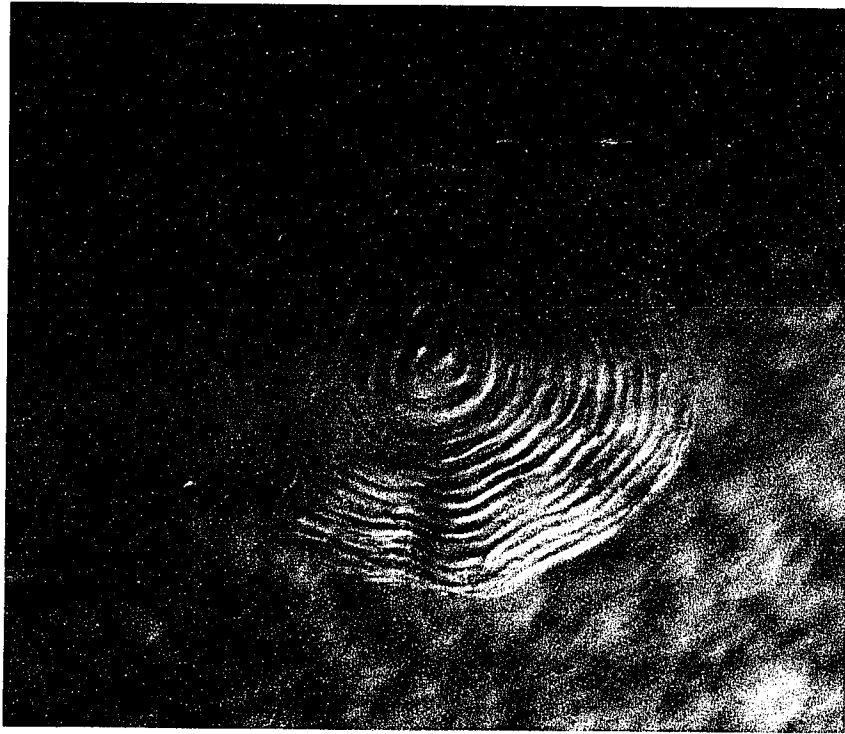


Figure 33



Figure 34

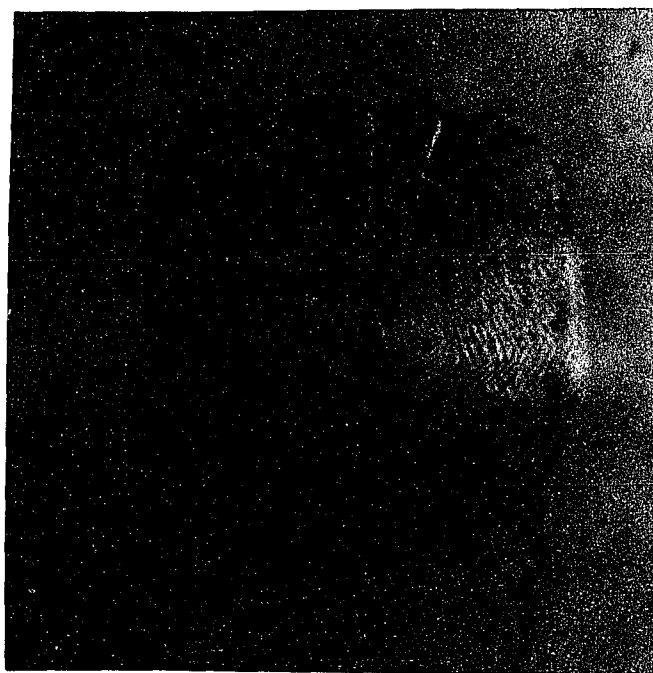


Figure 35



Figure 36

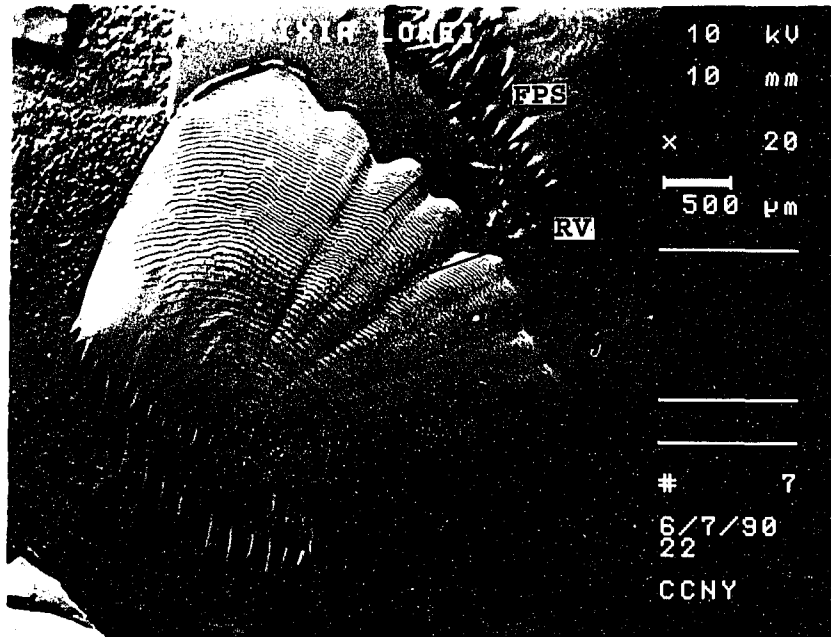


Figure 37



Figure 38

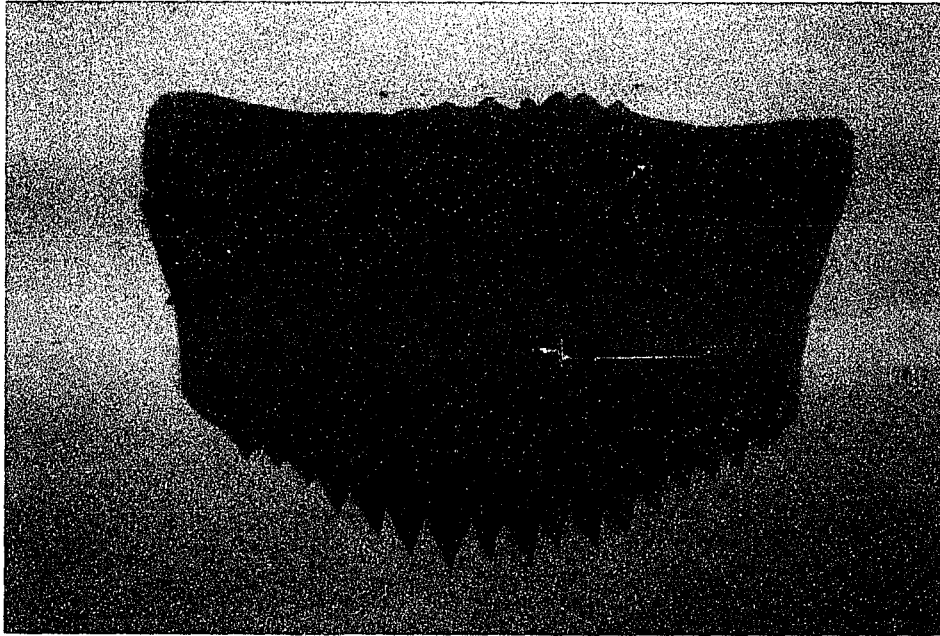


Figure 39



Figure 40

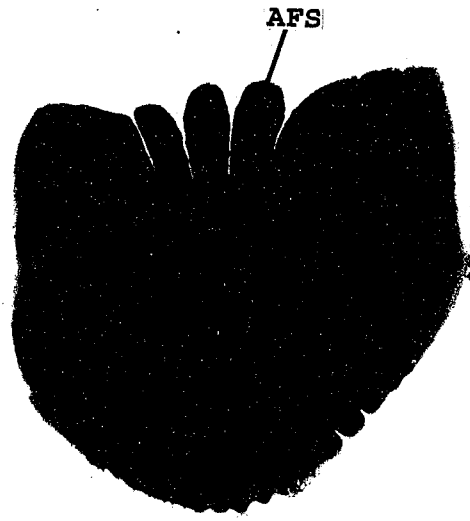


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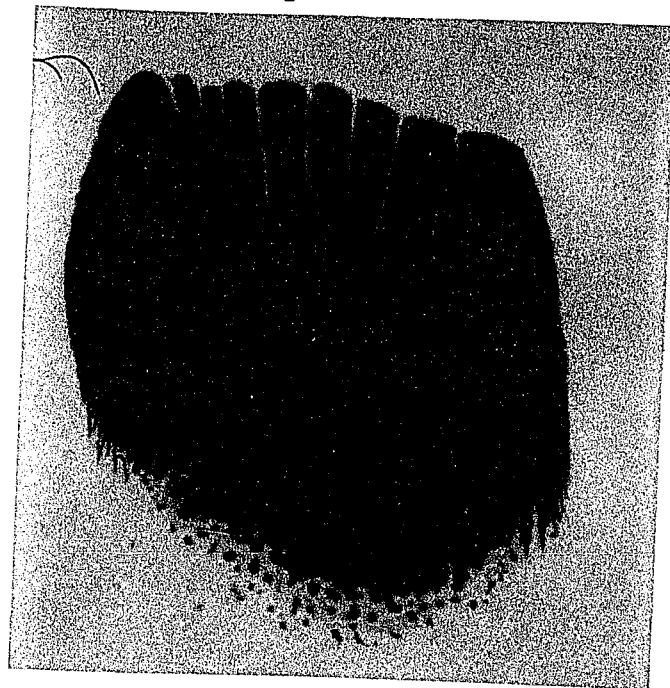


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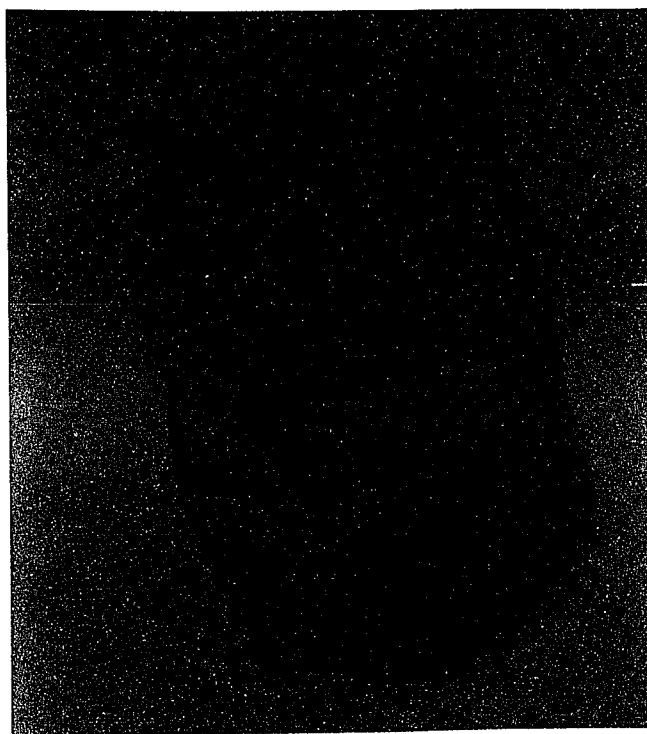


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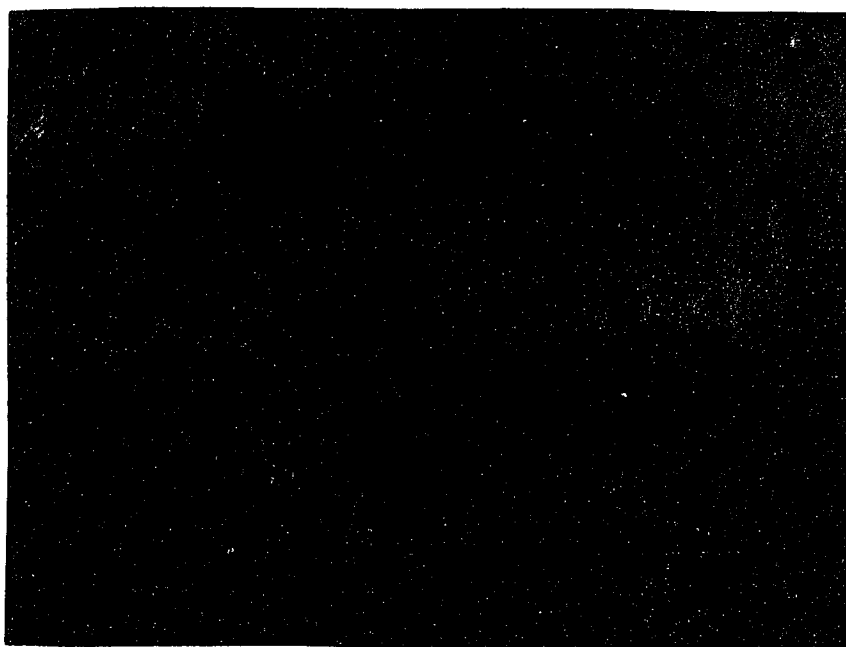


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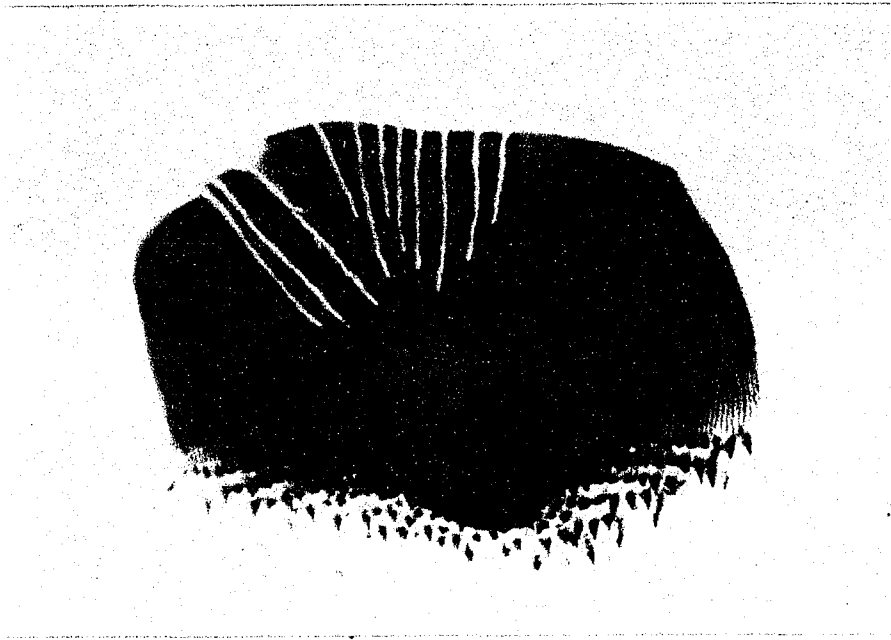


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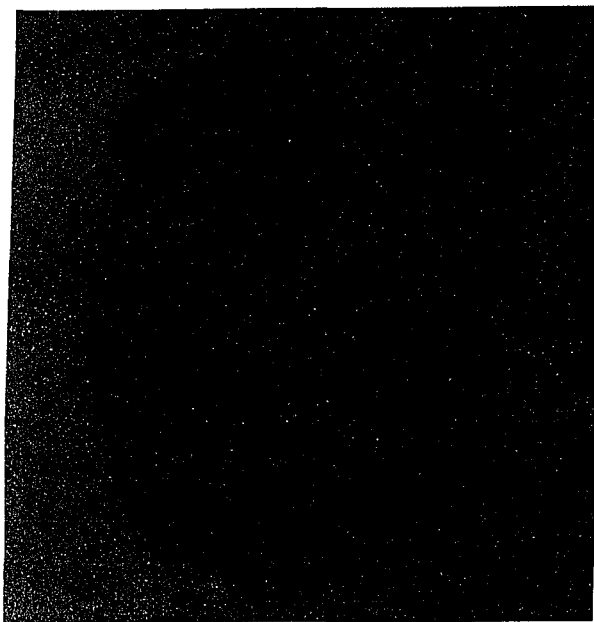


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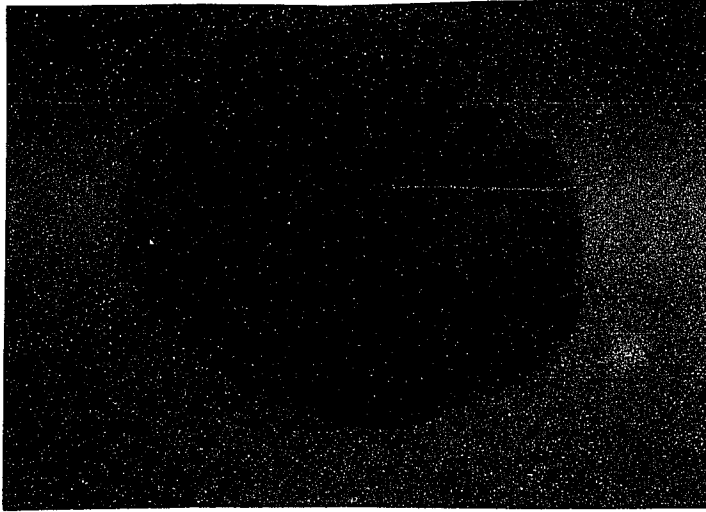


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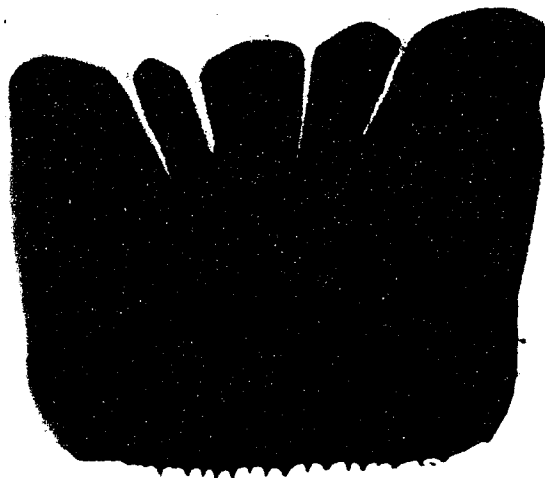


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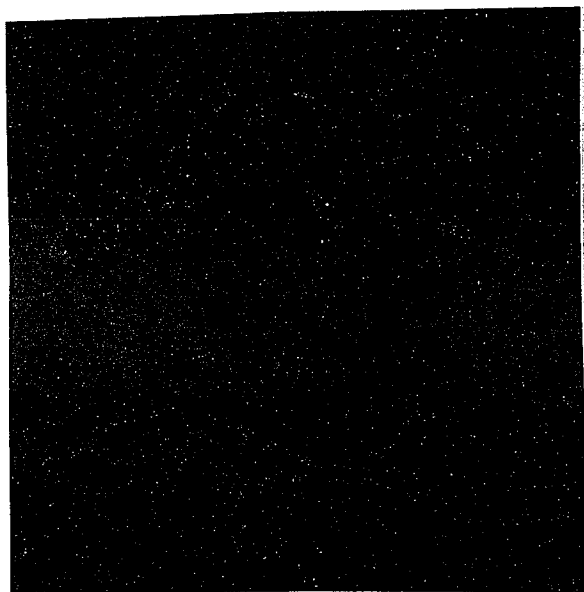


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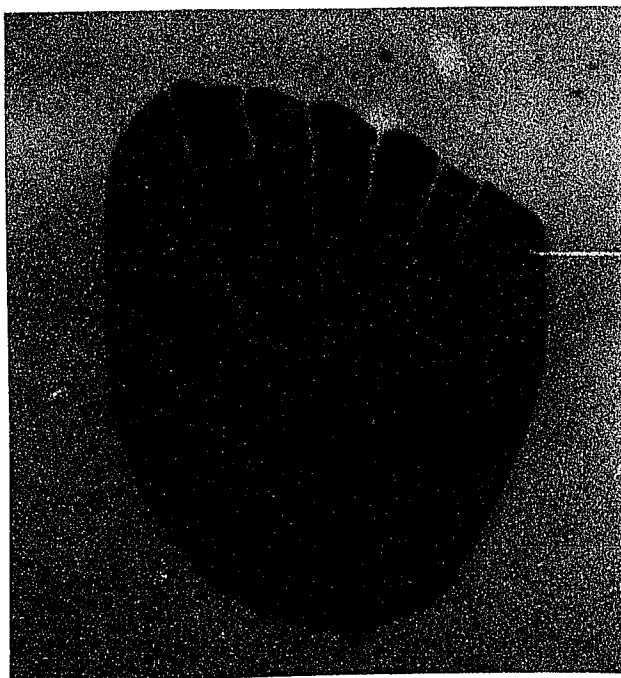


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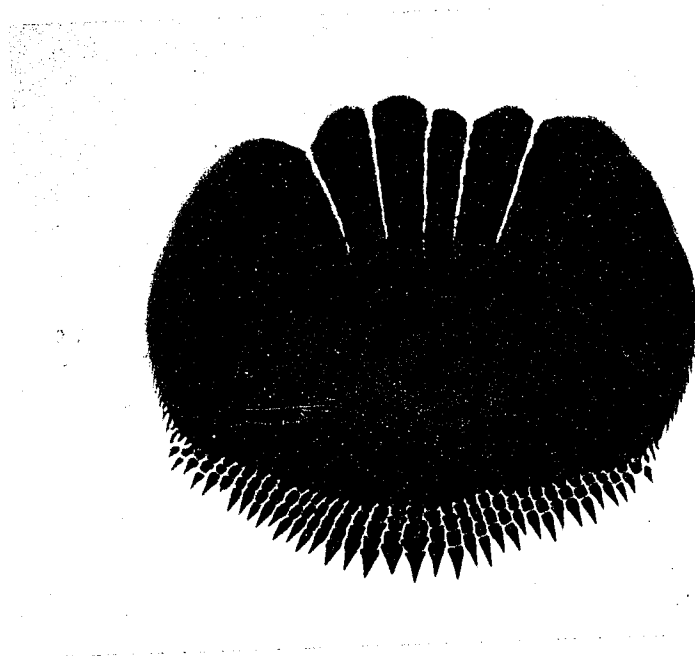


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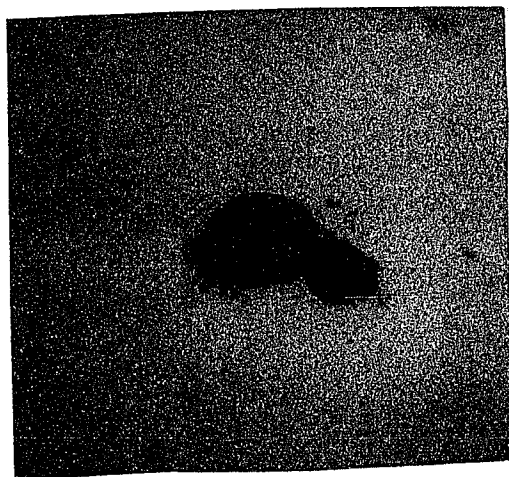


Figure 52



Figure 53

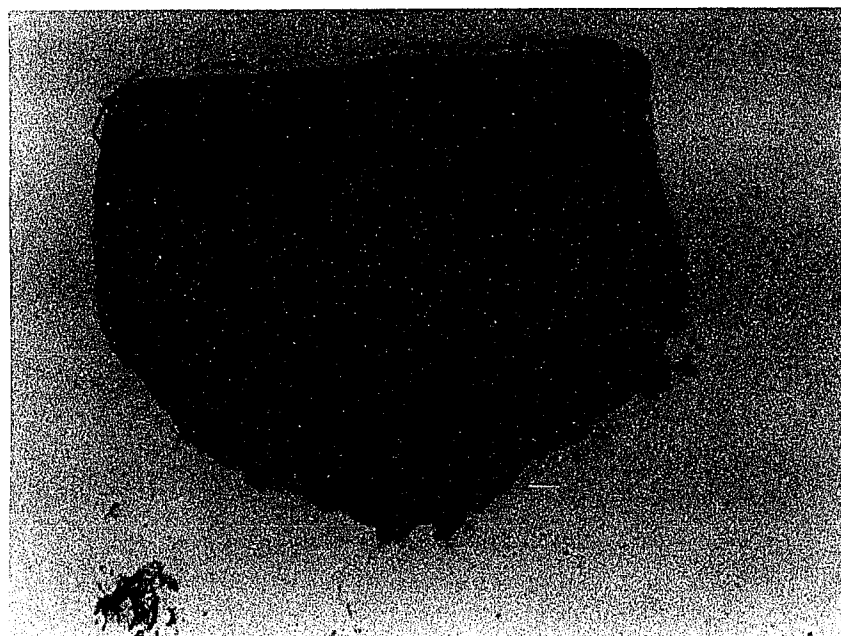


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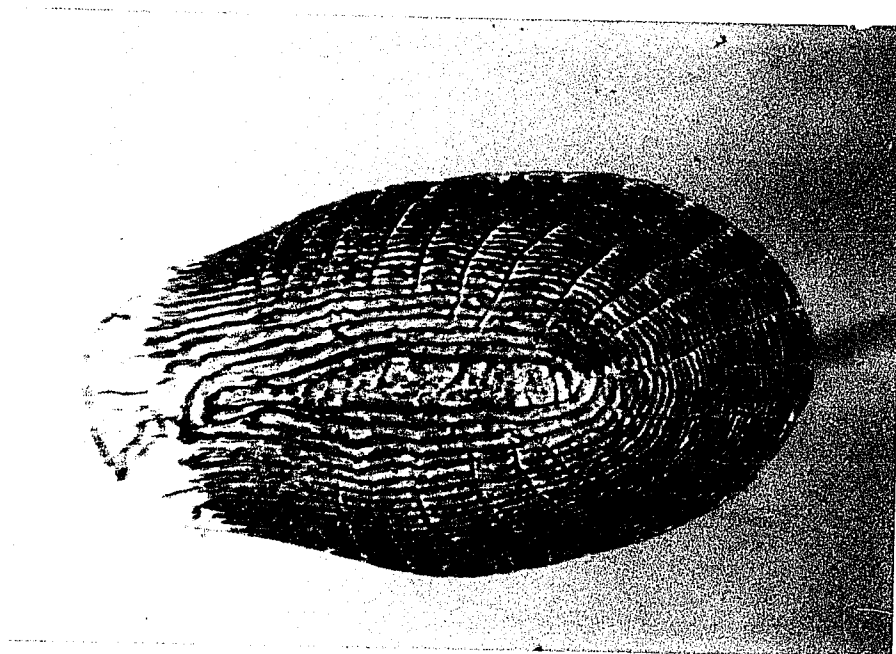


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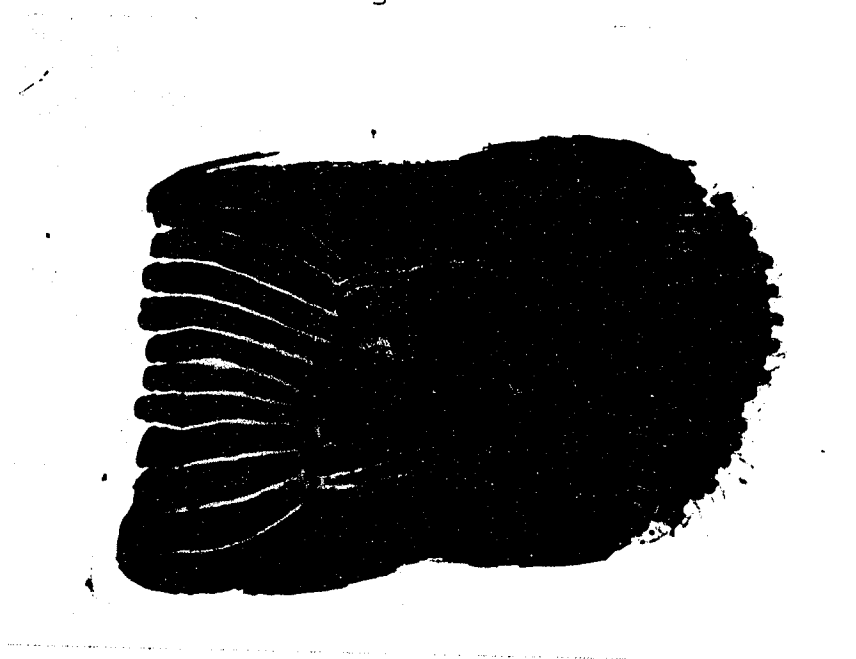


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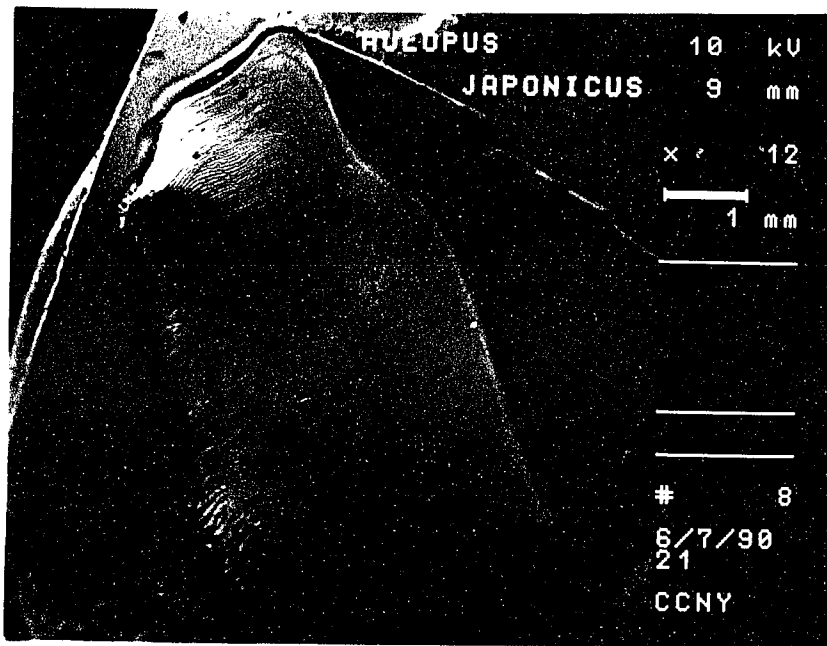


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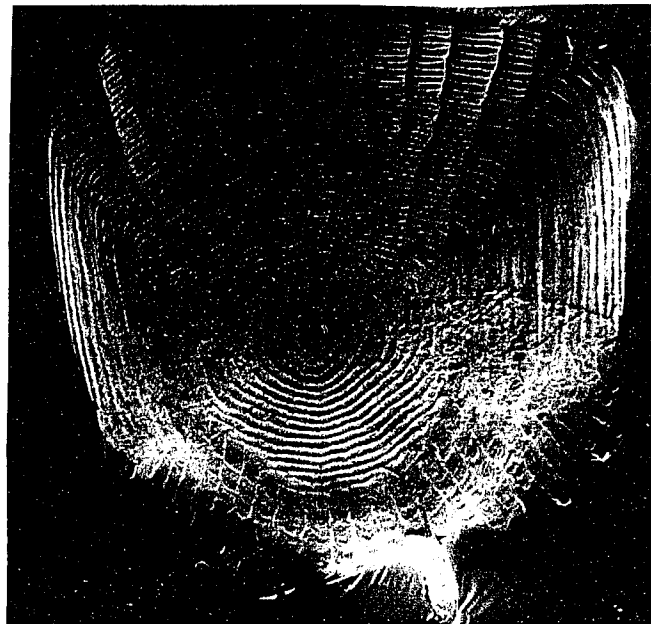


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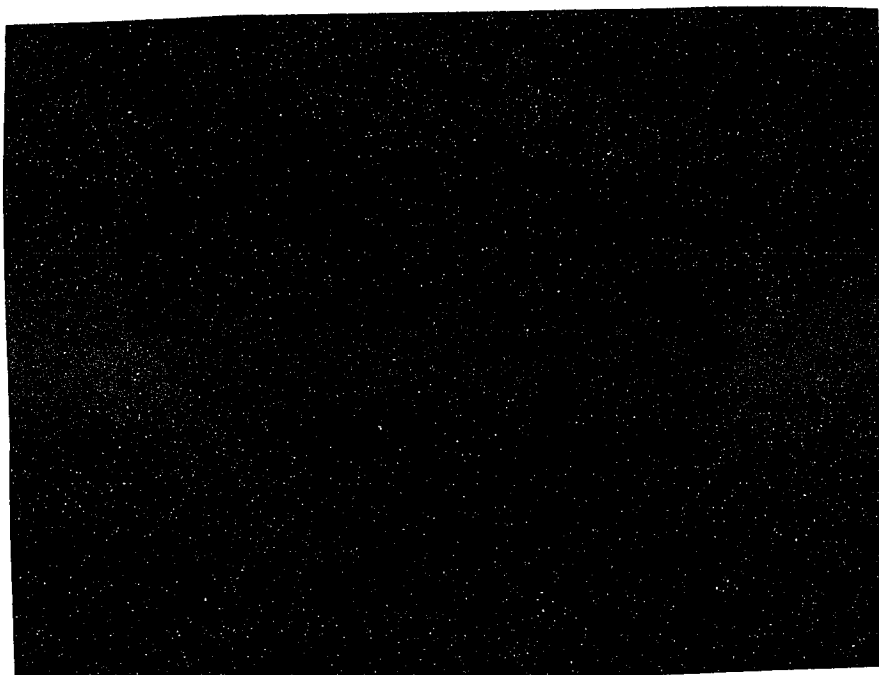


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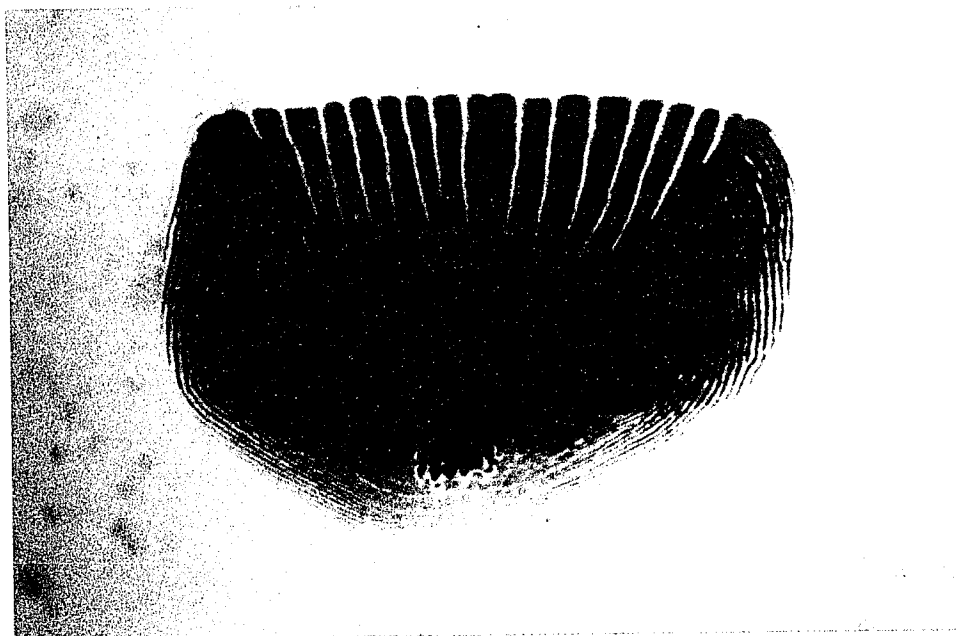


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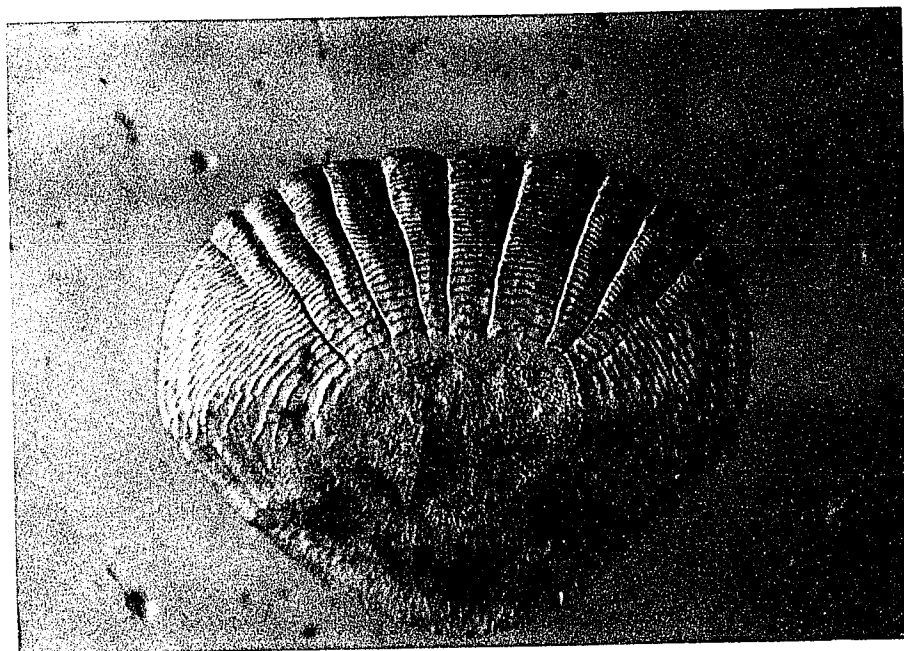


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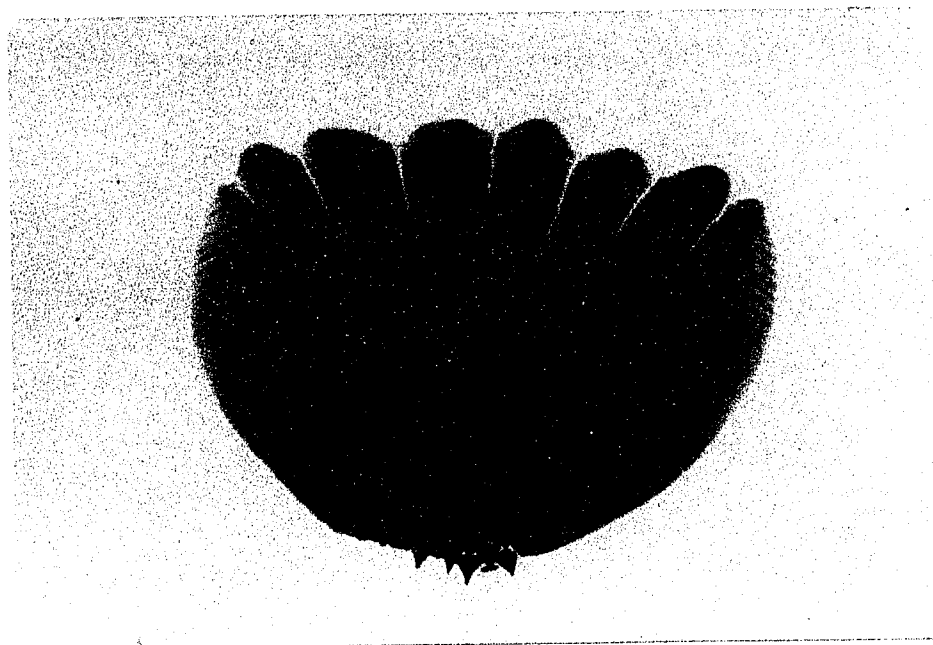


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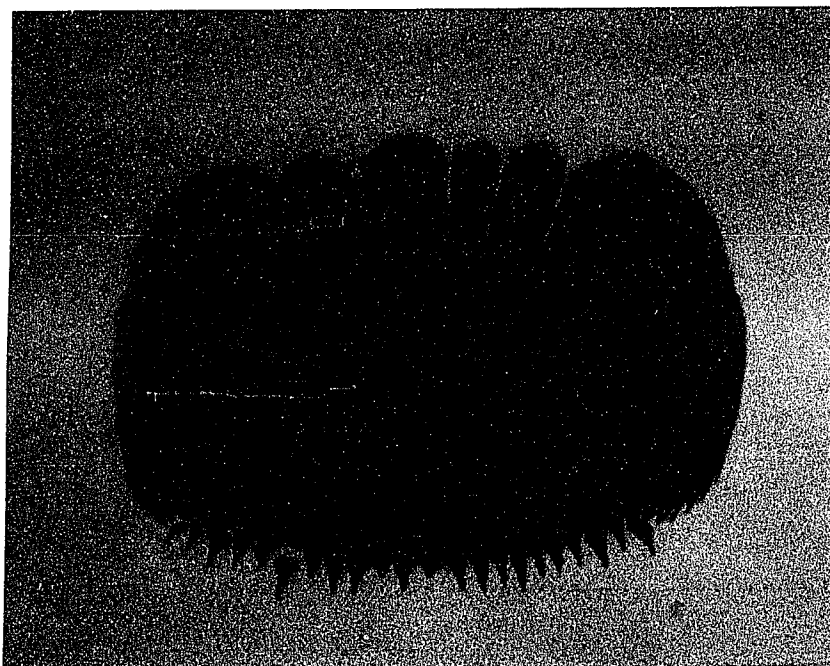


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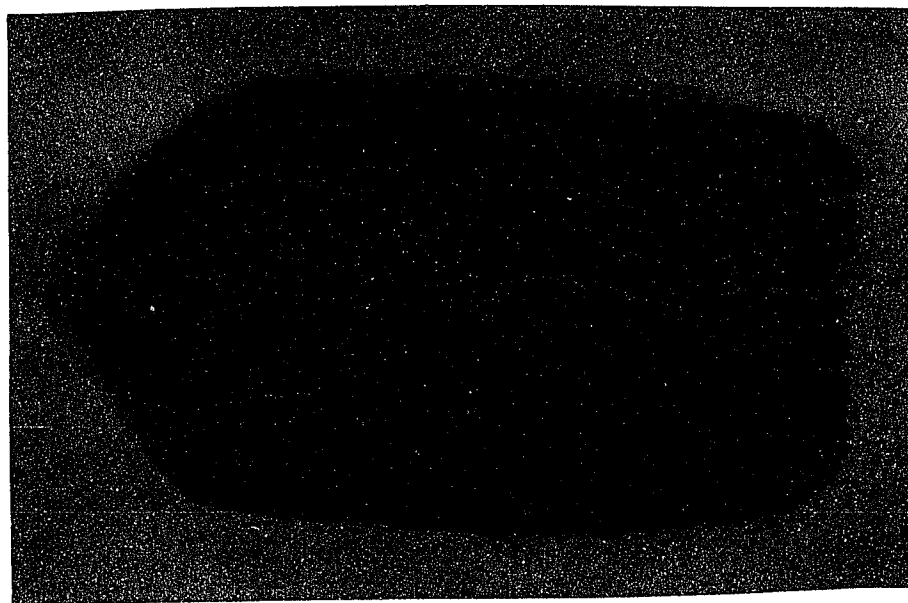


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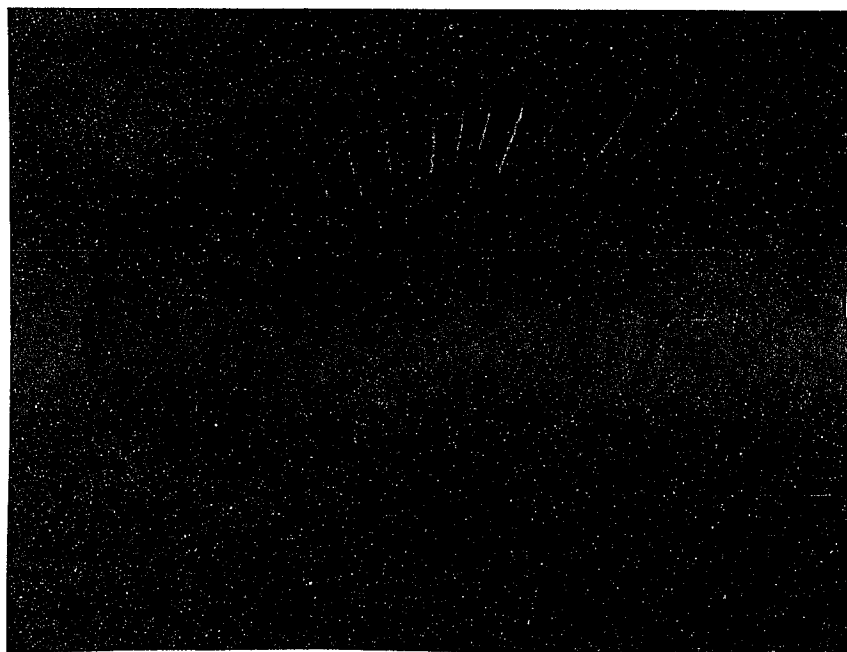


Figure 65



Figure 66

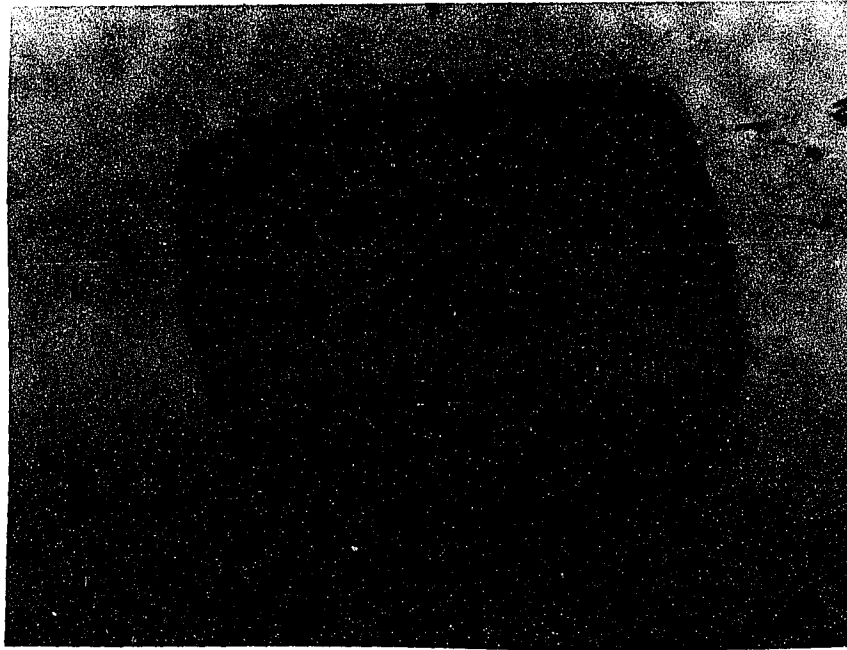


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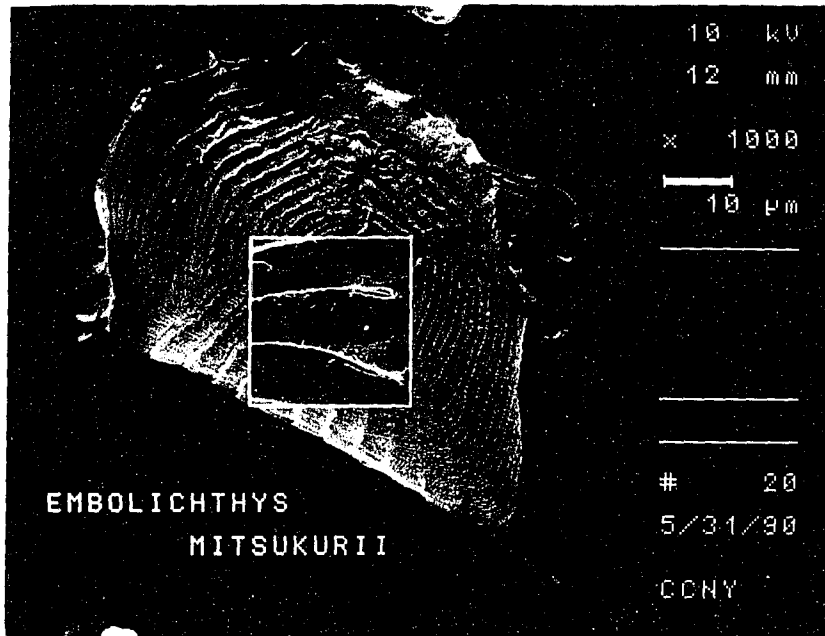


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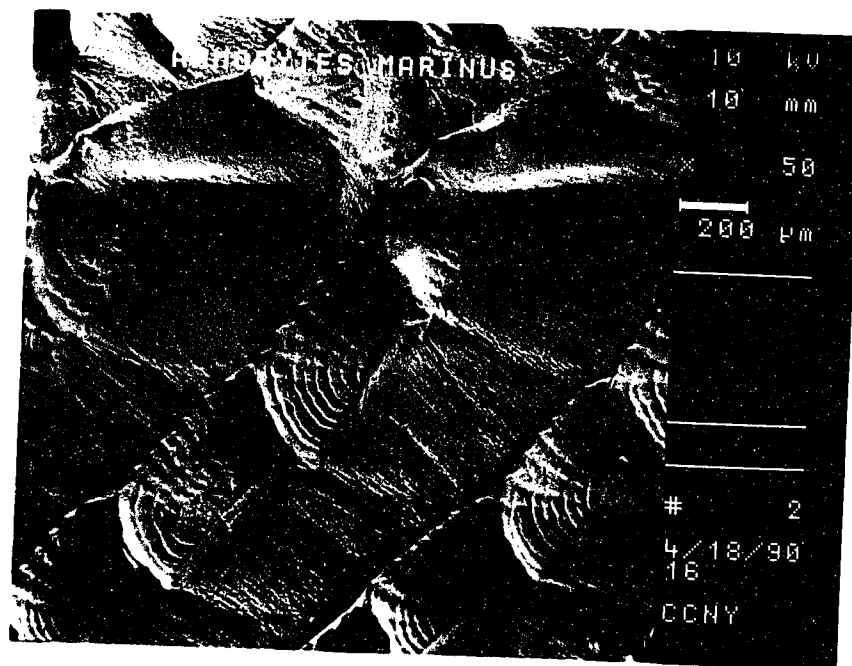


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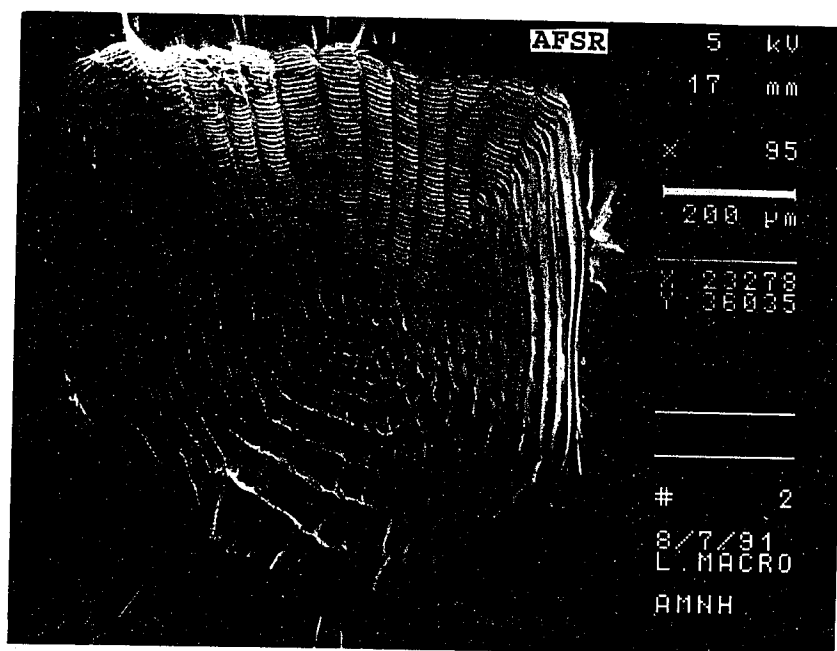


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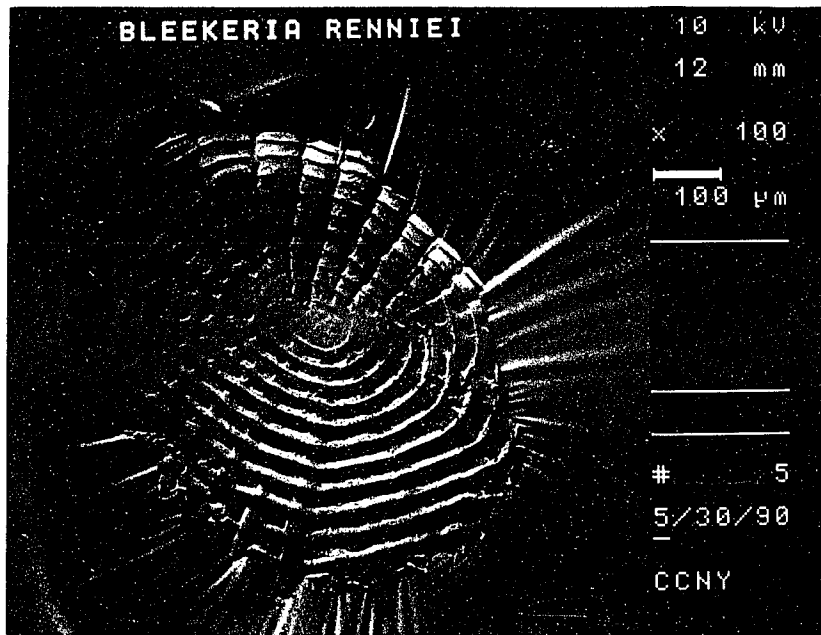


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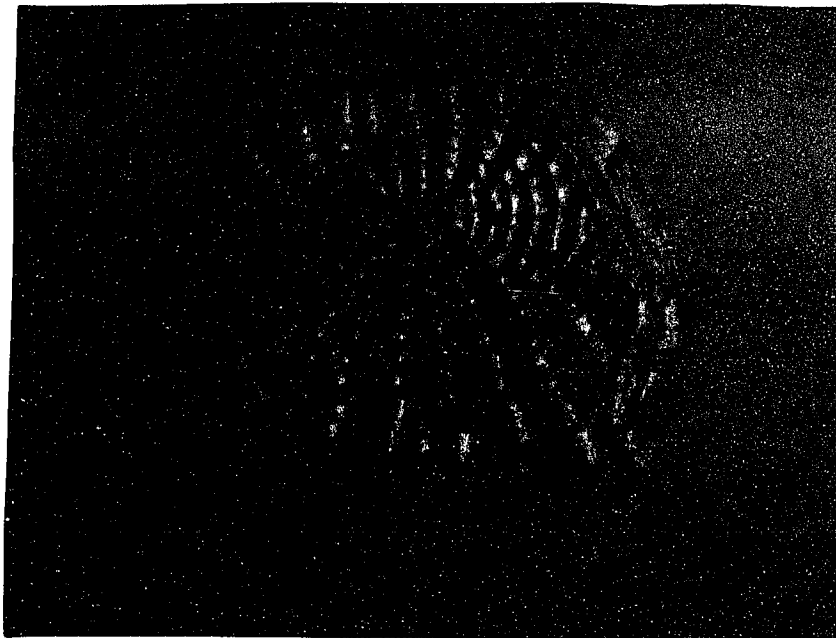


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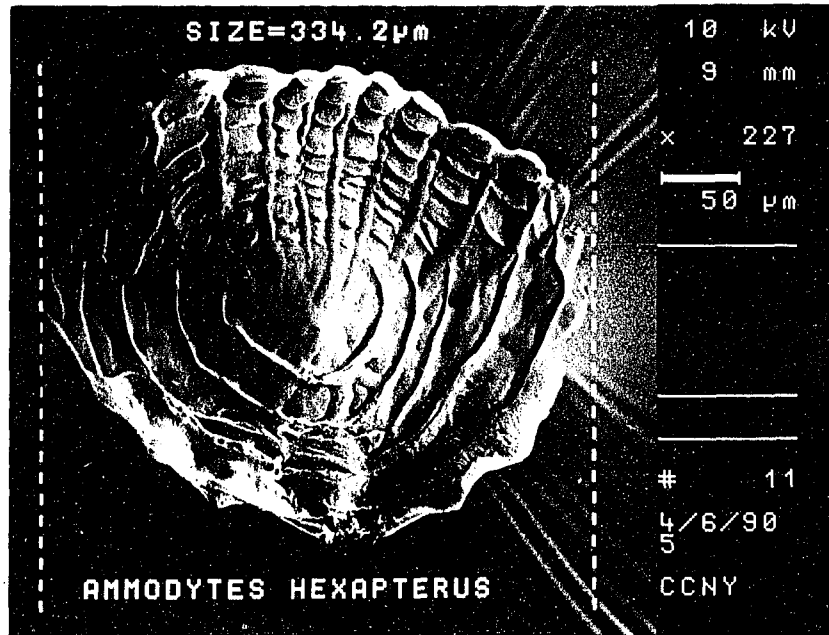


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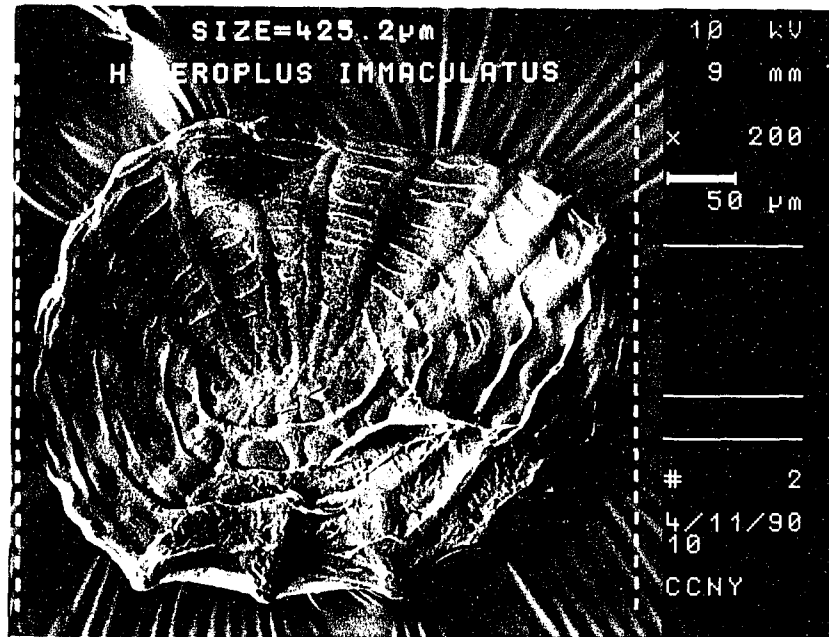


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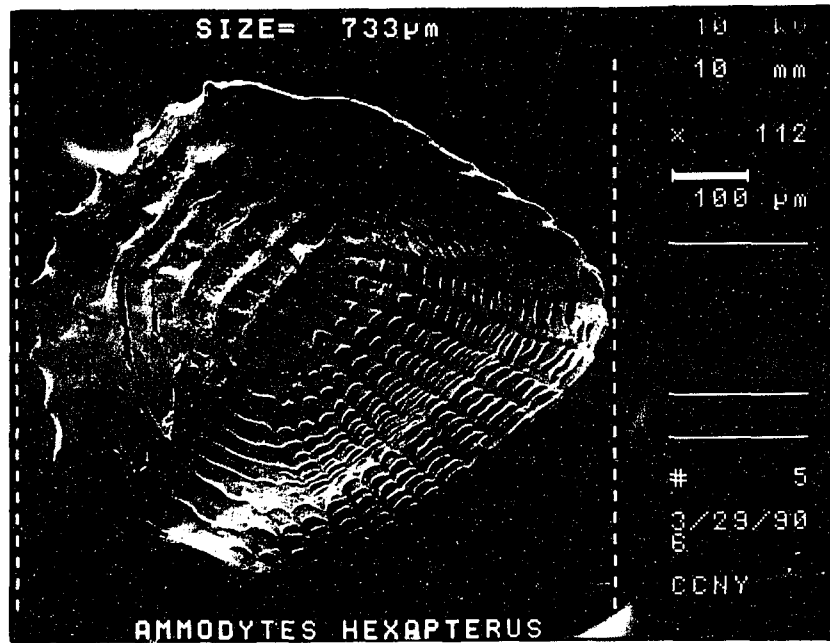


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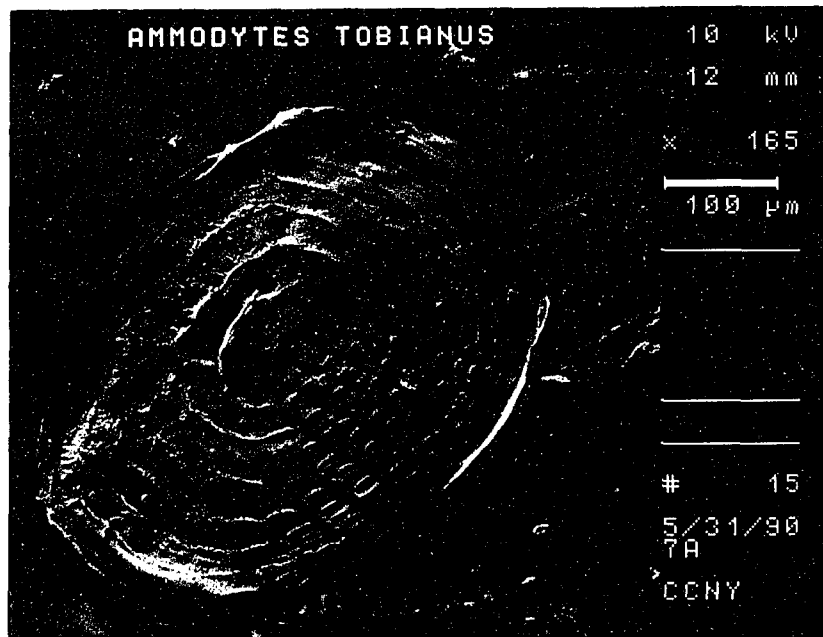


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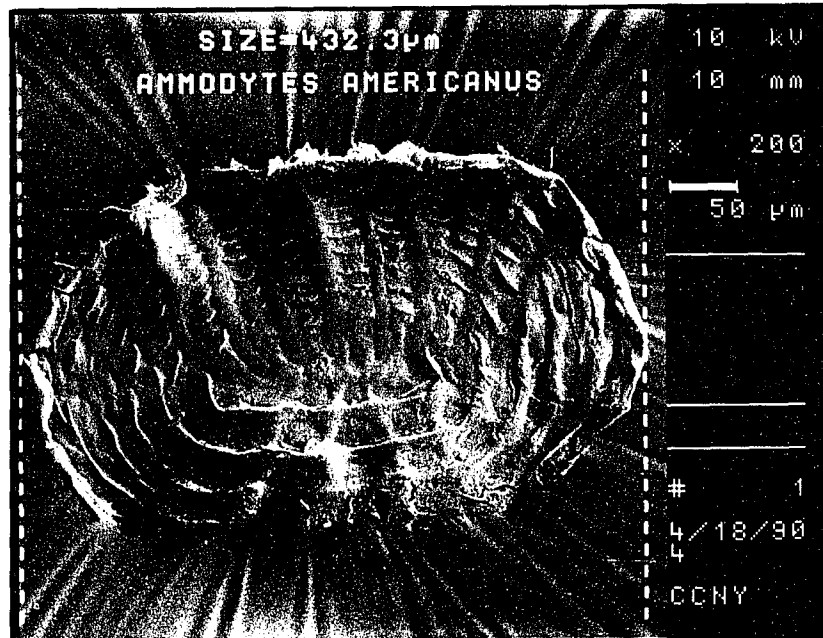


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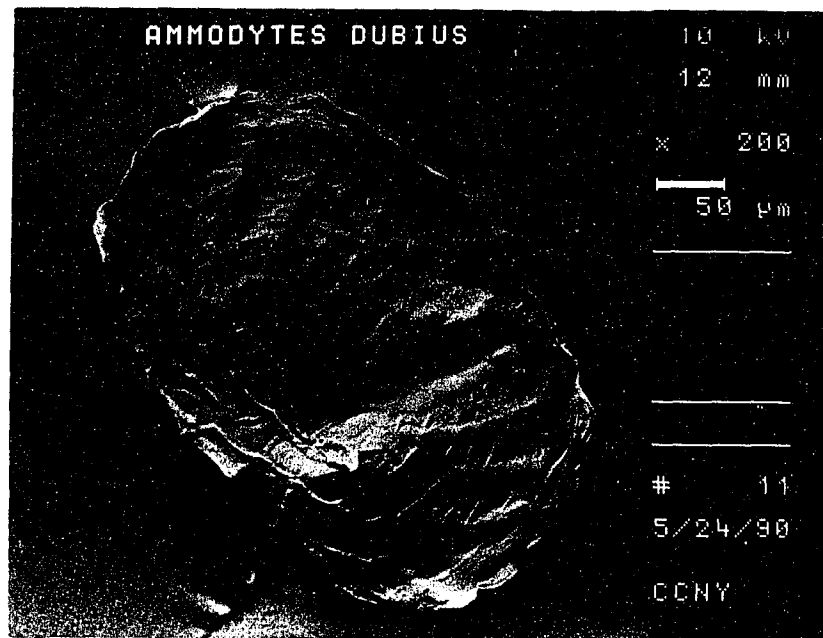


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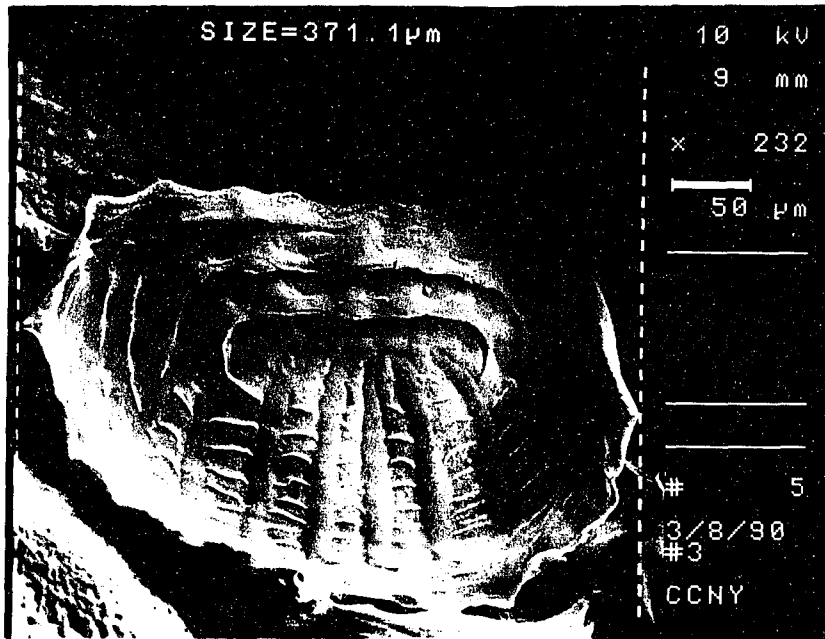


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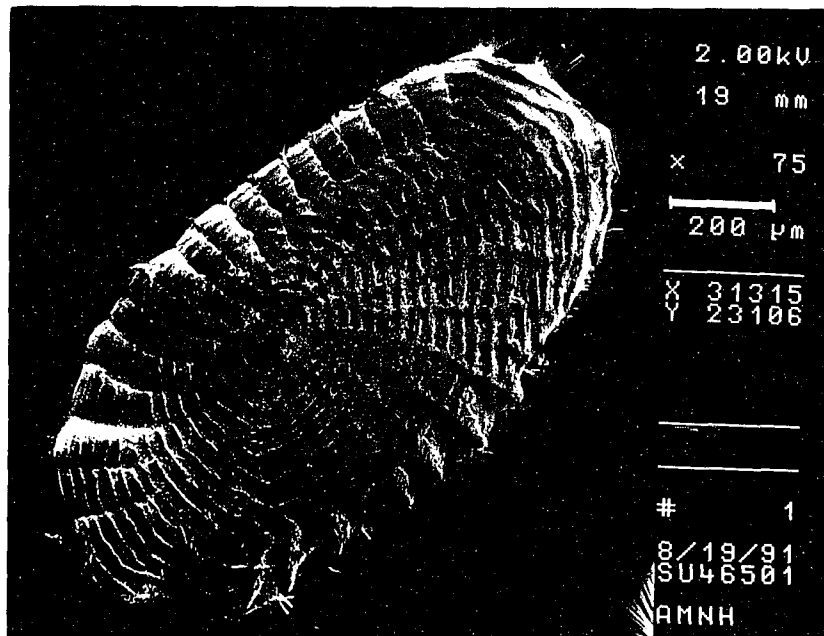


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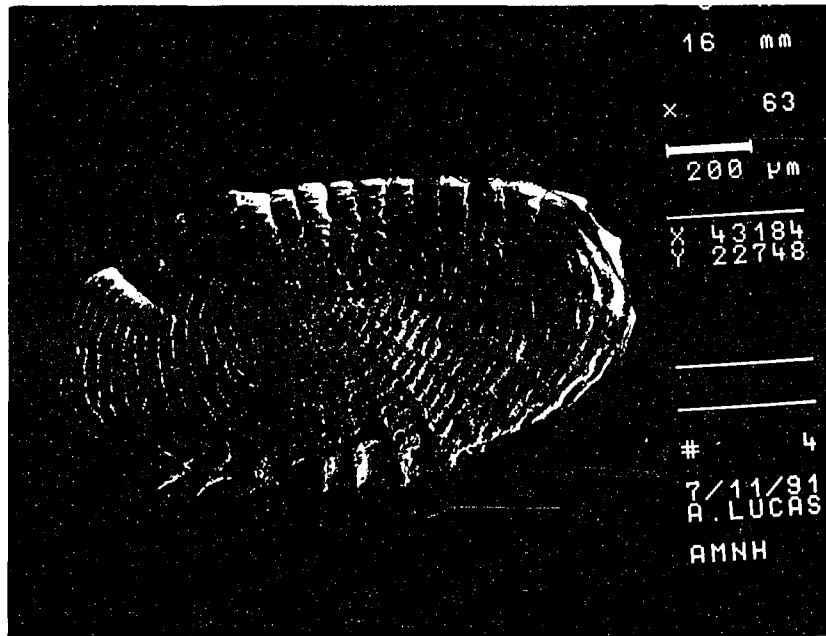


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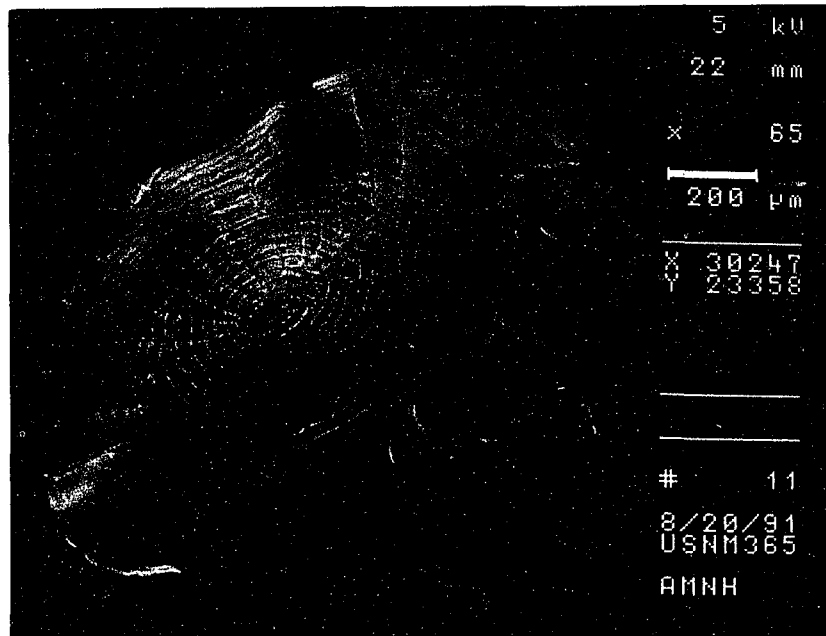


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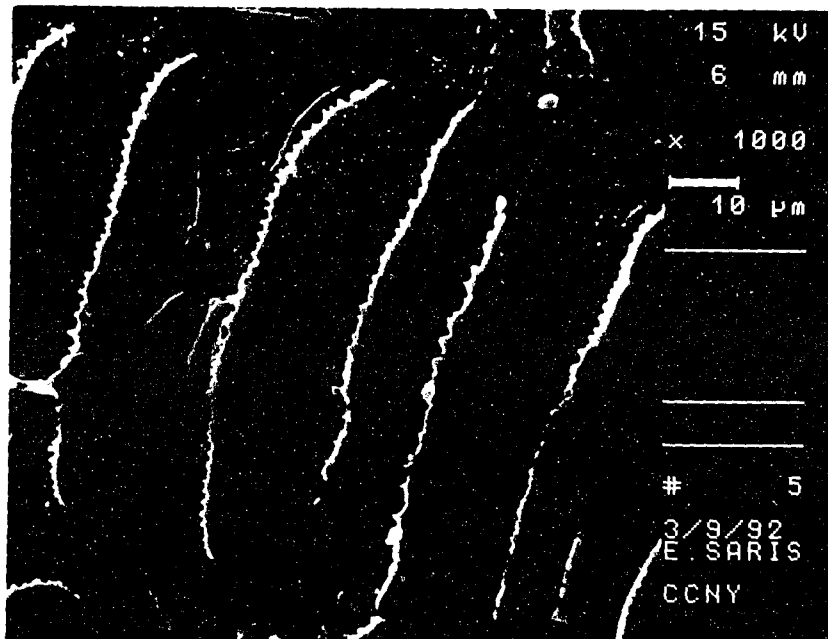


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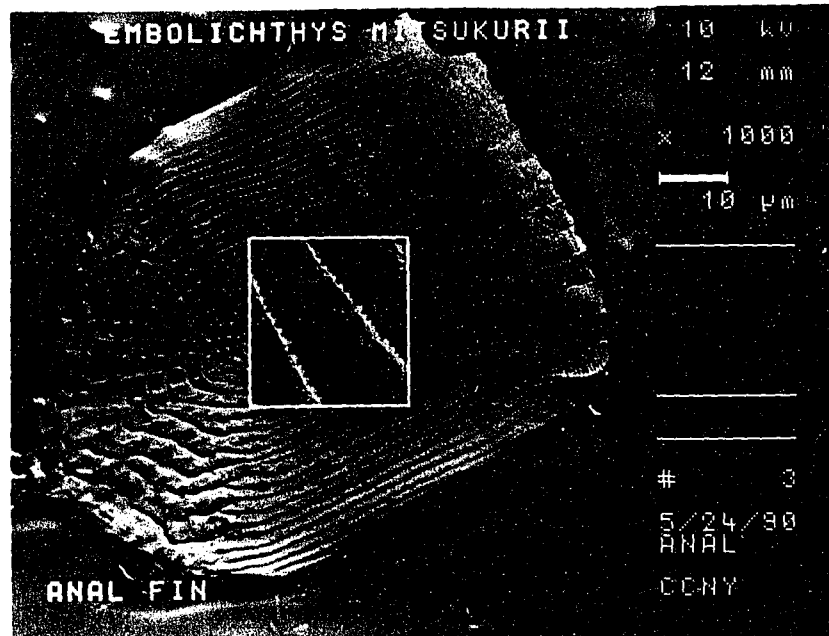


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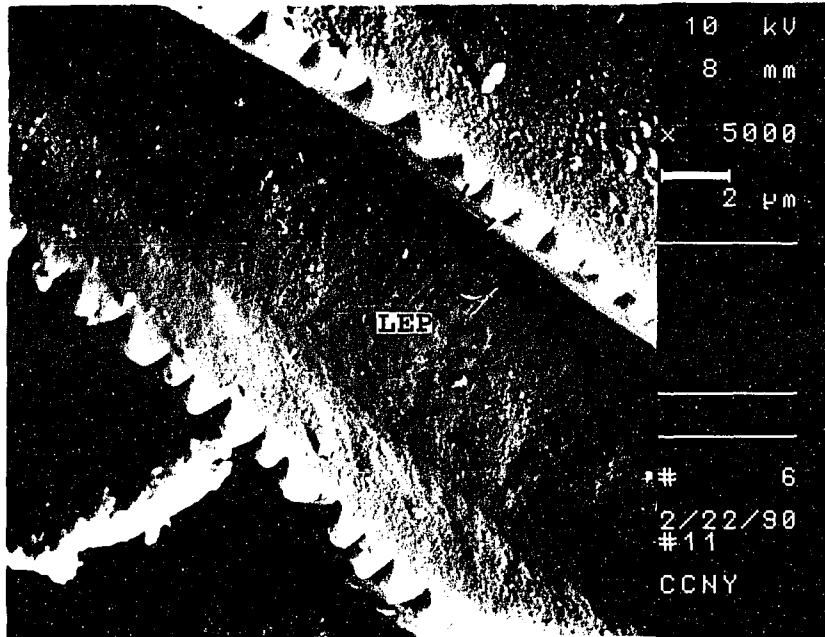


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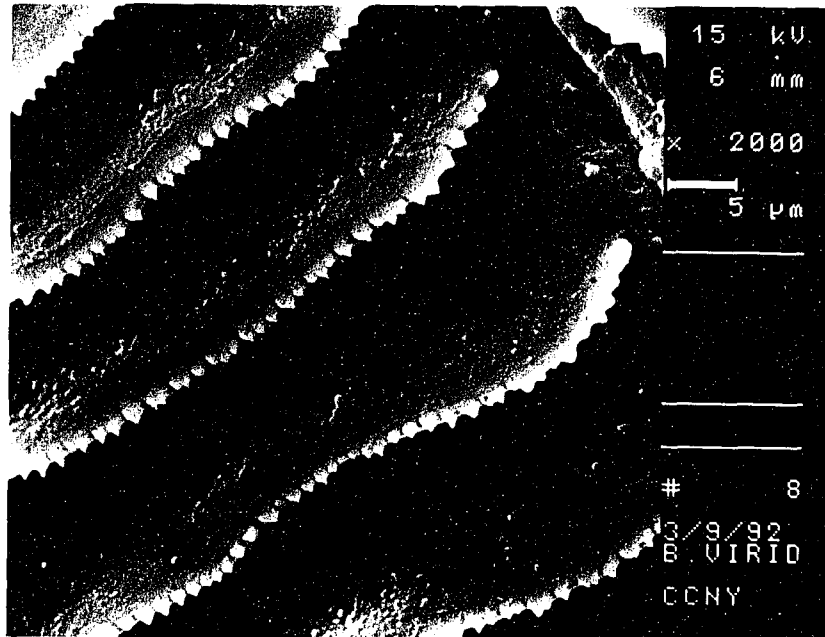


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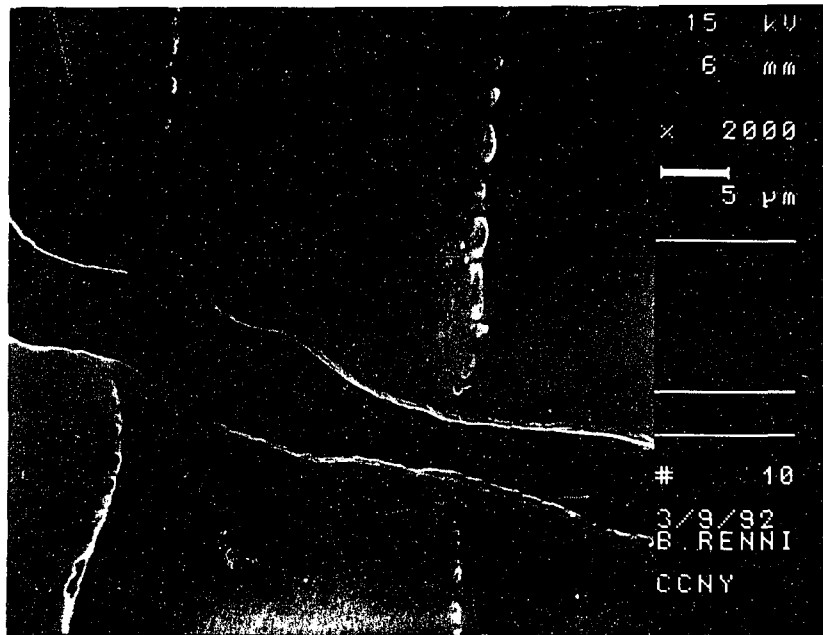


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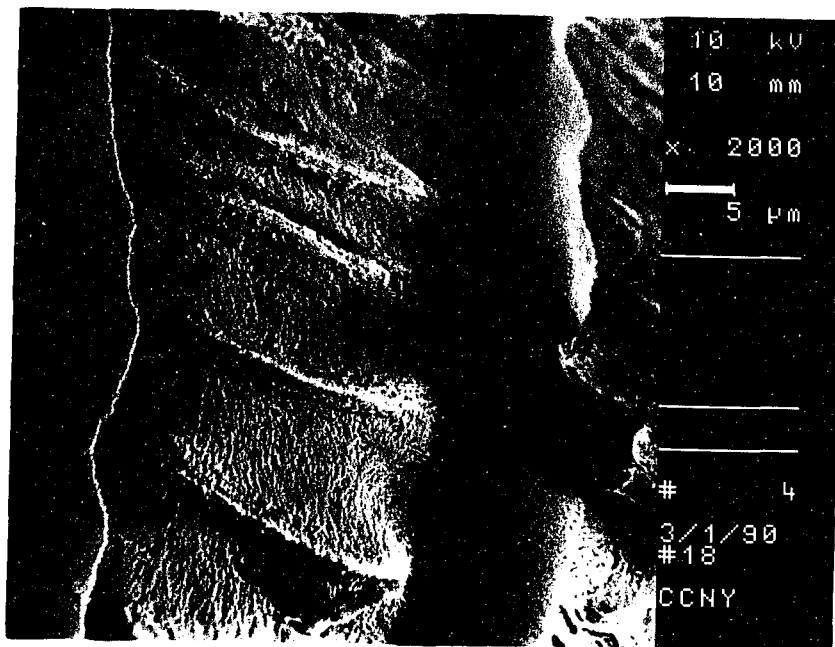


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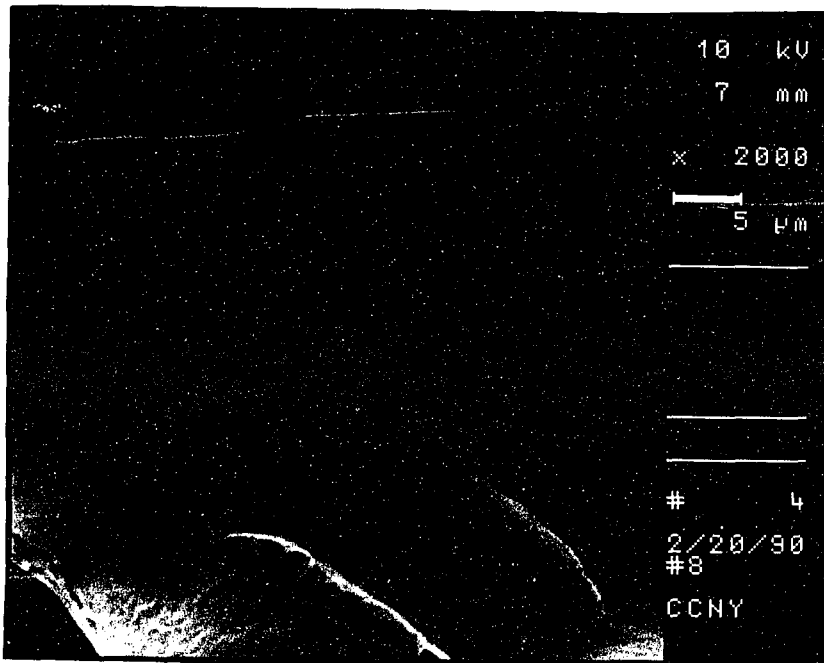


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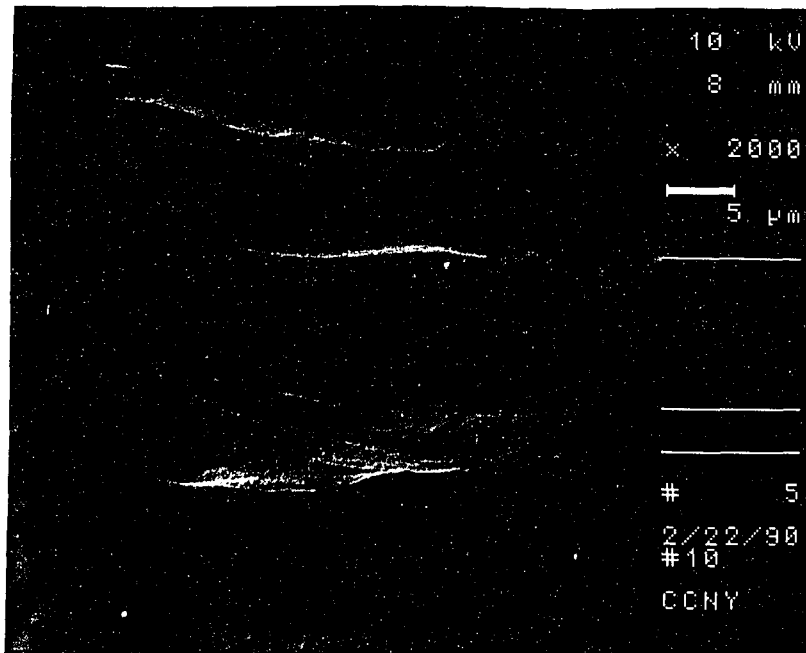


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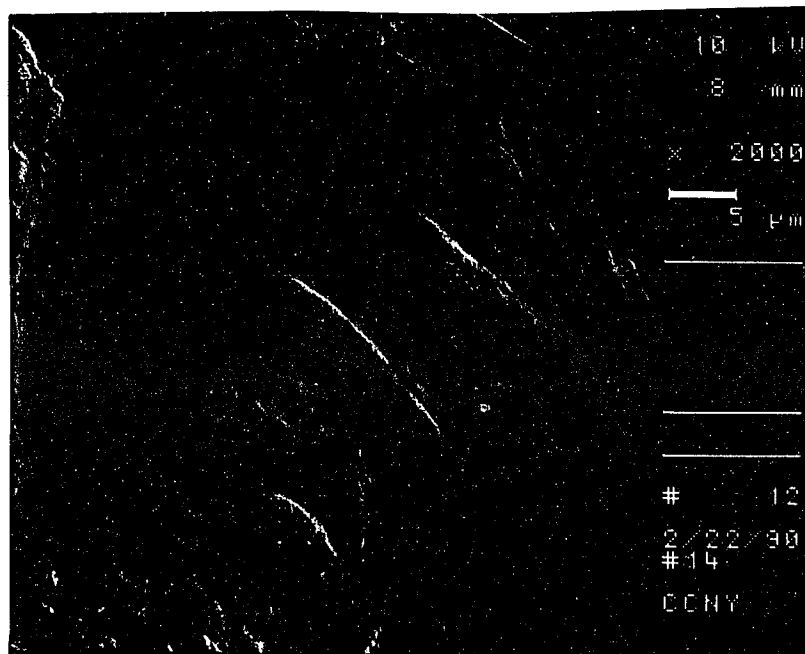


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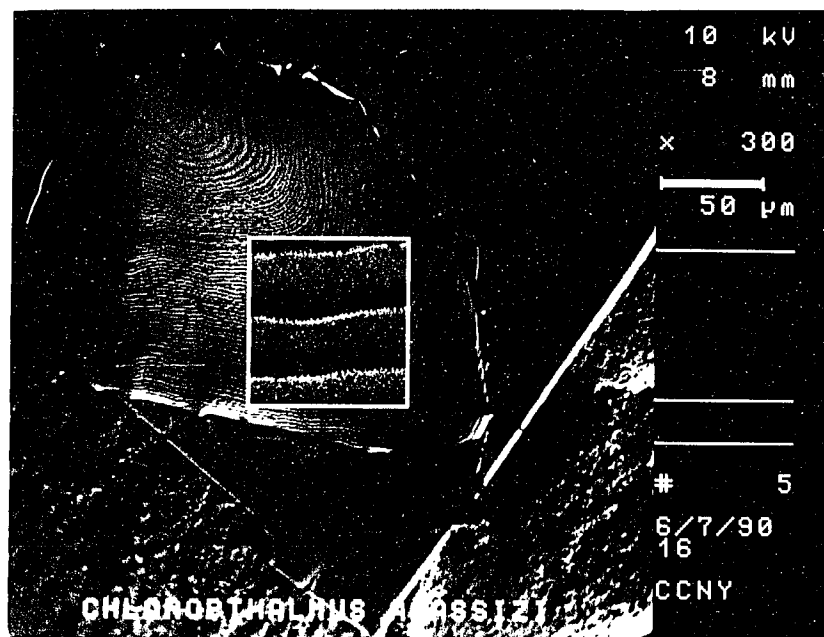


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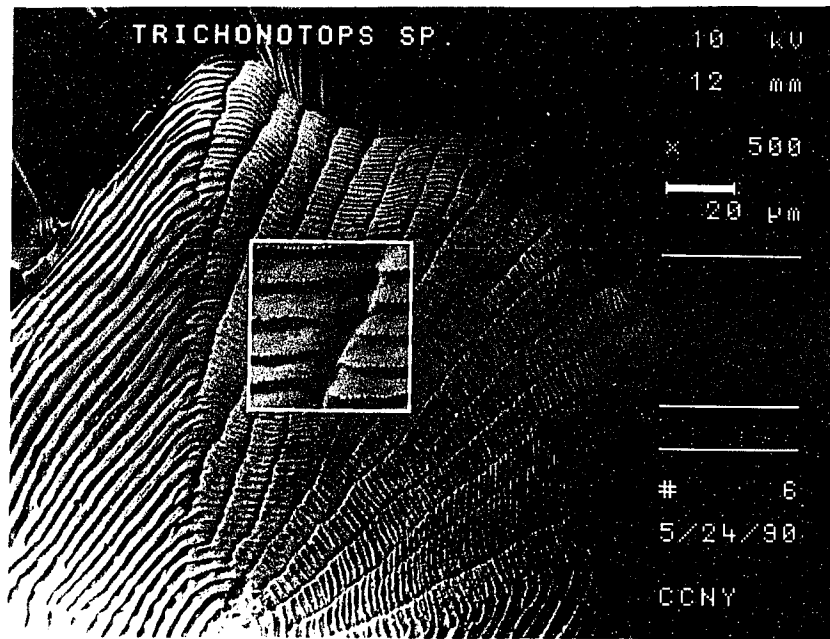


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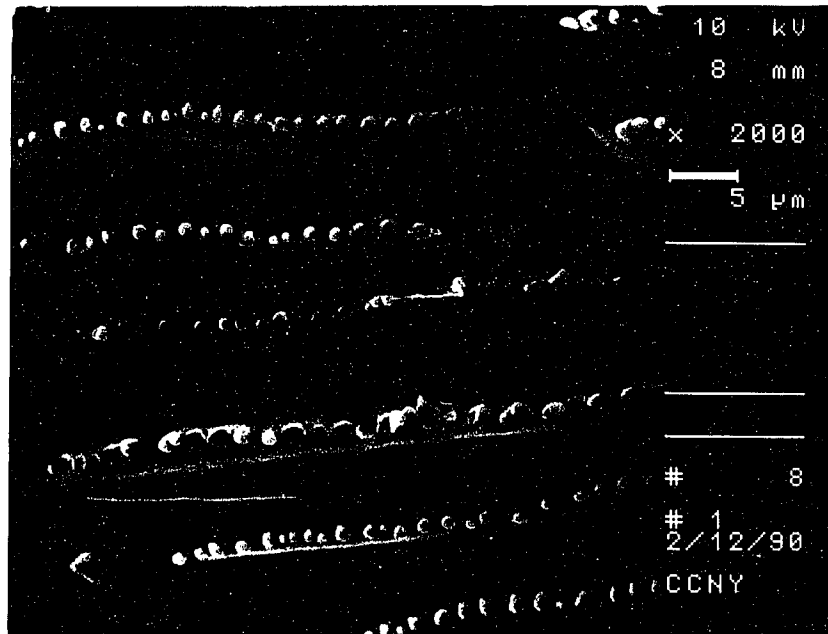


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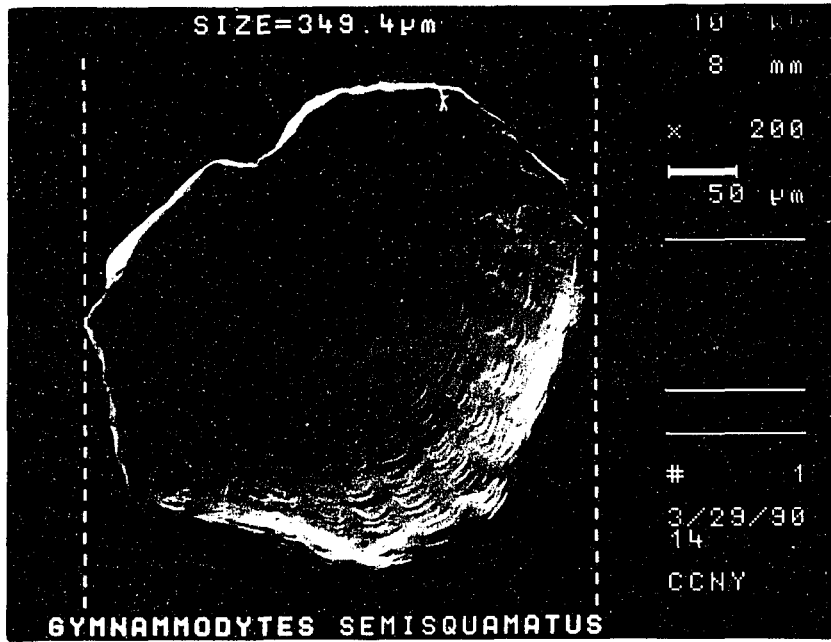


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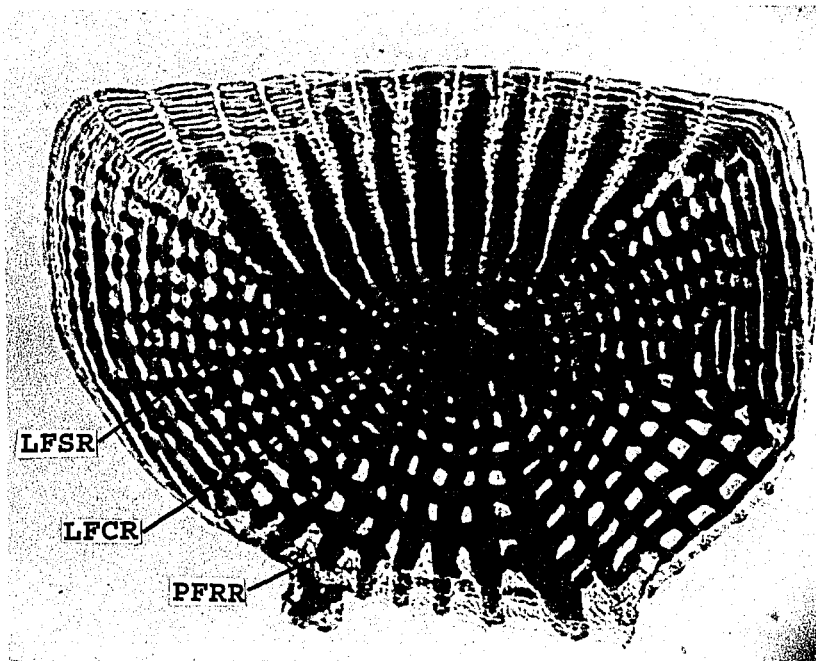


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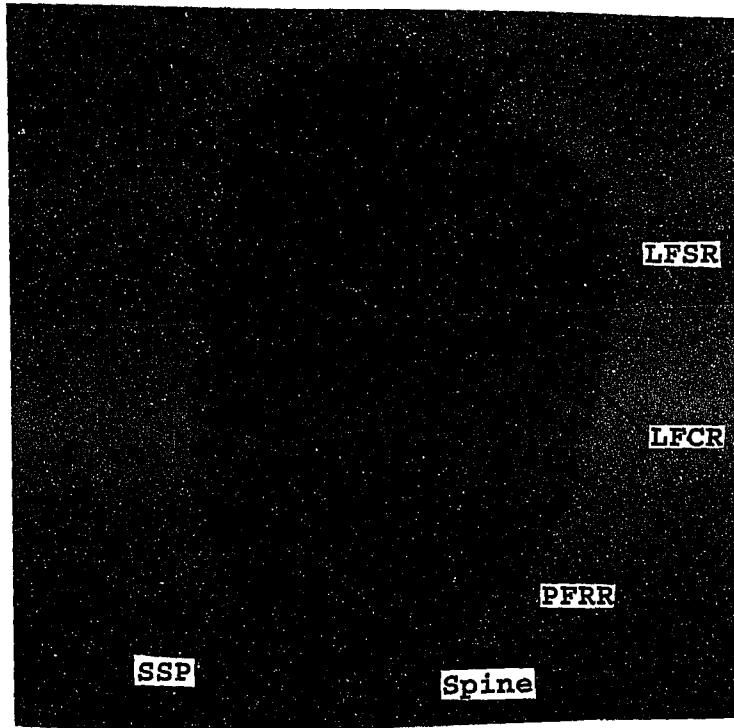


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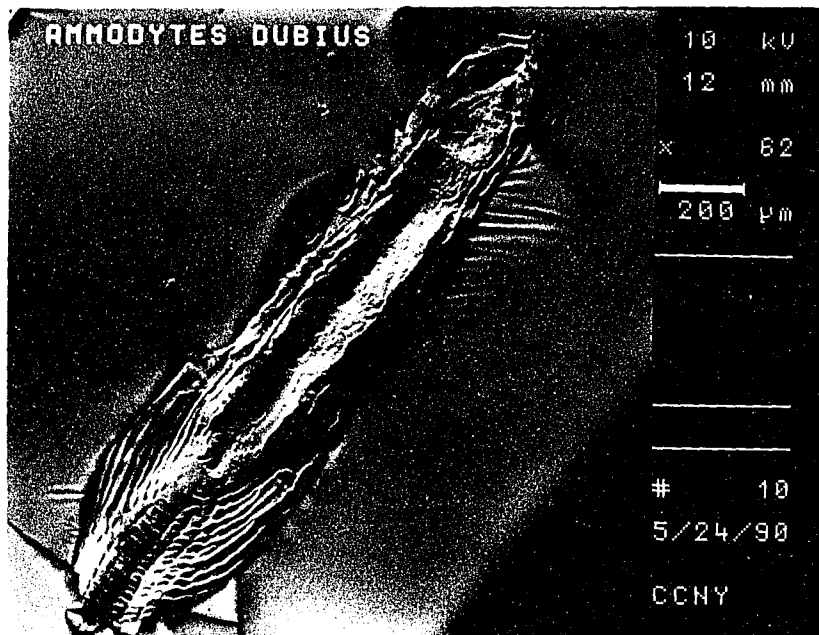


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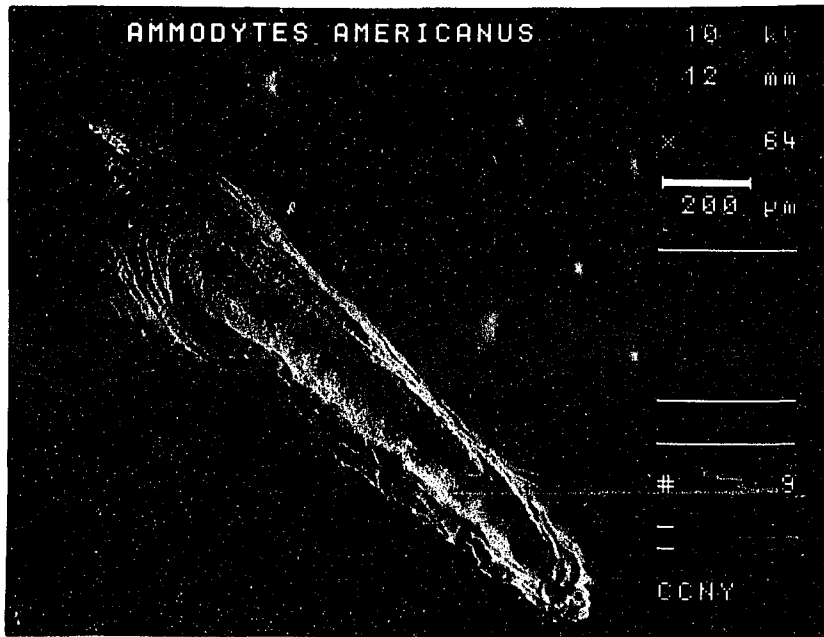


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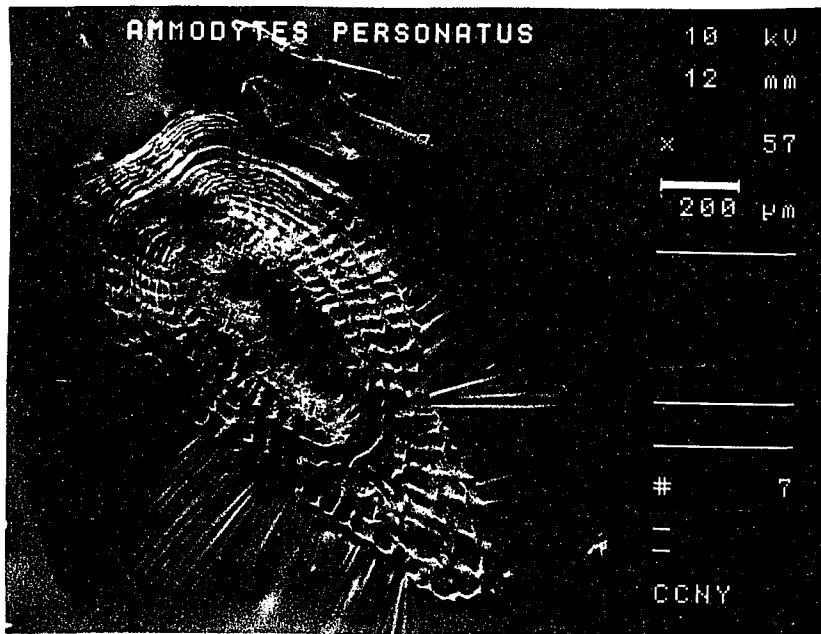


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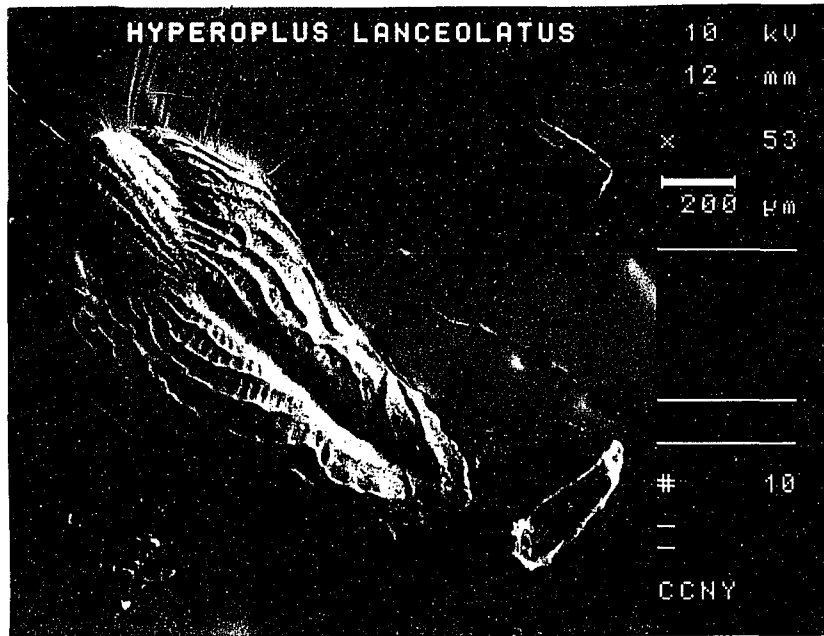


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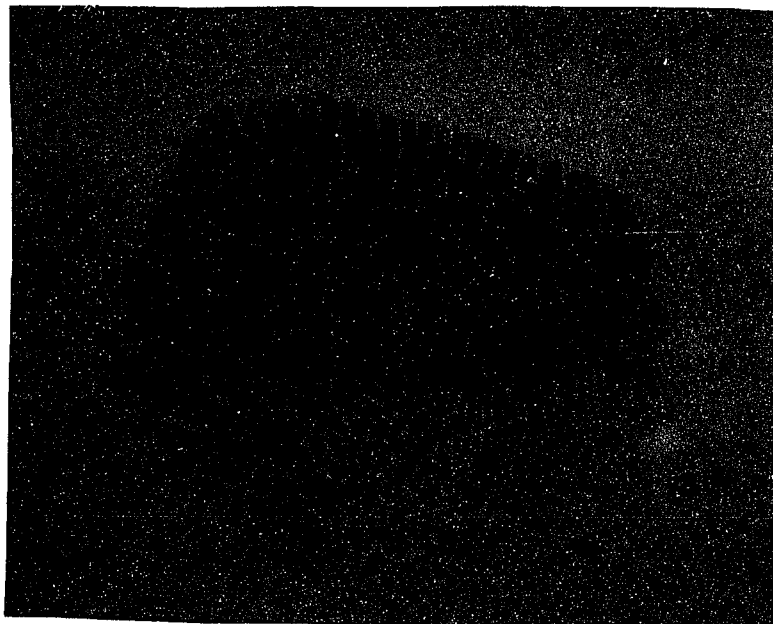


Figure 102

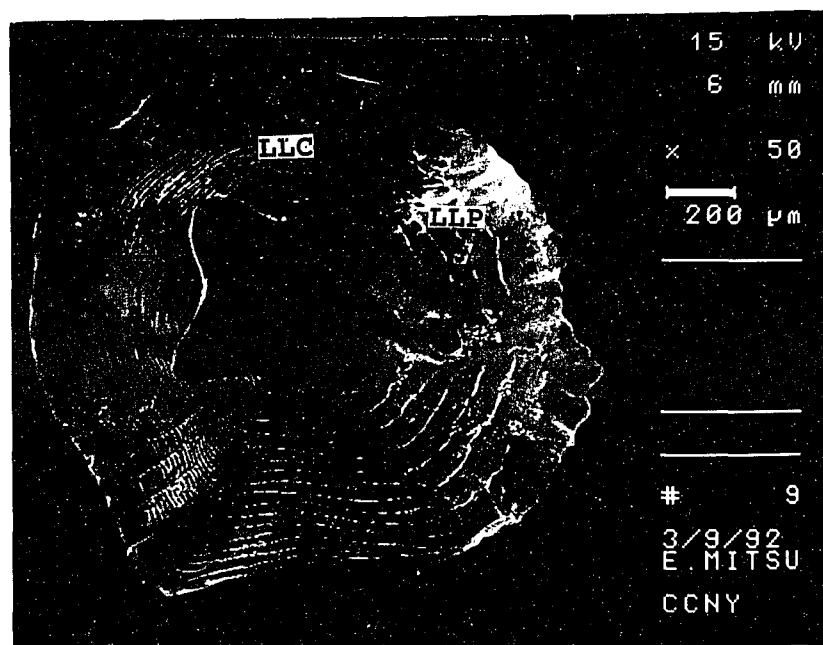


Figure 103

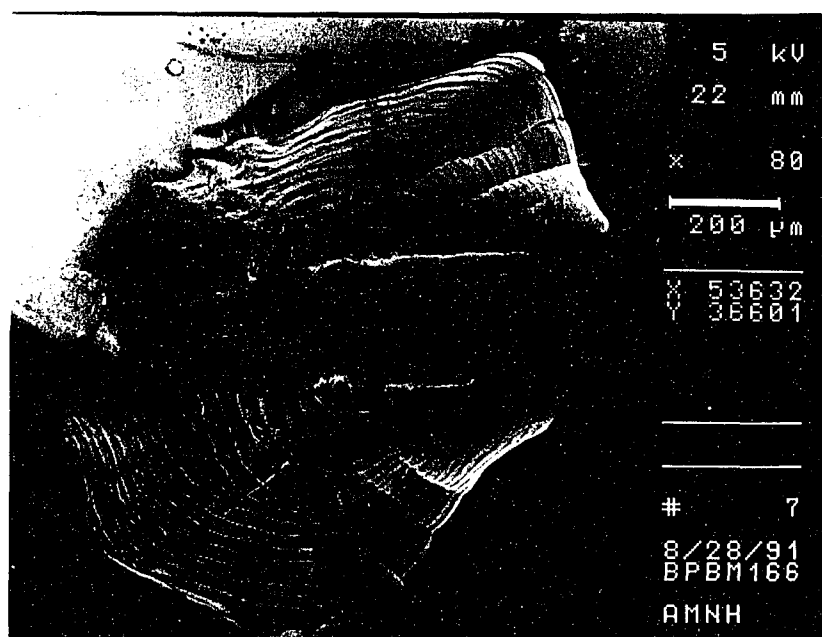


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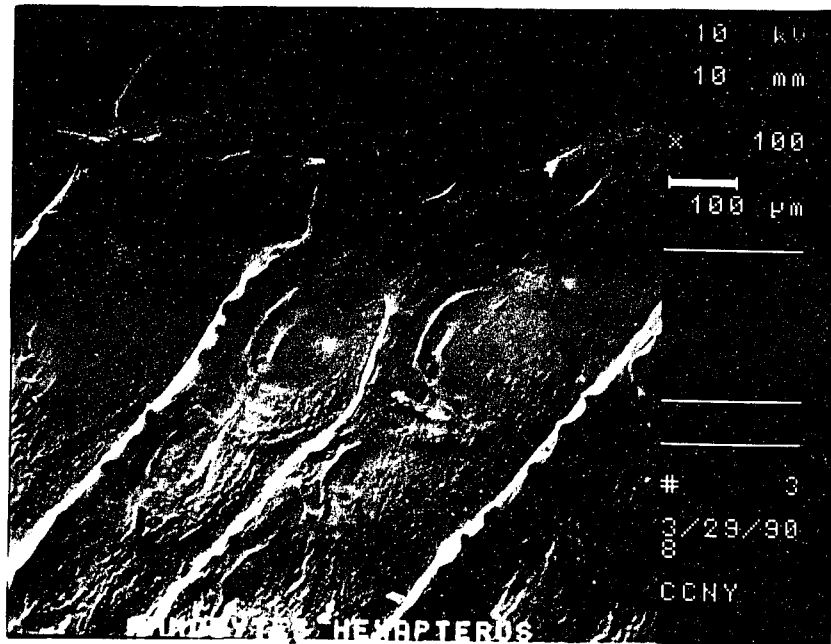


Figure 105

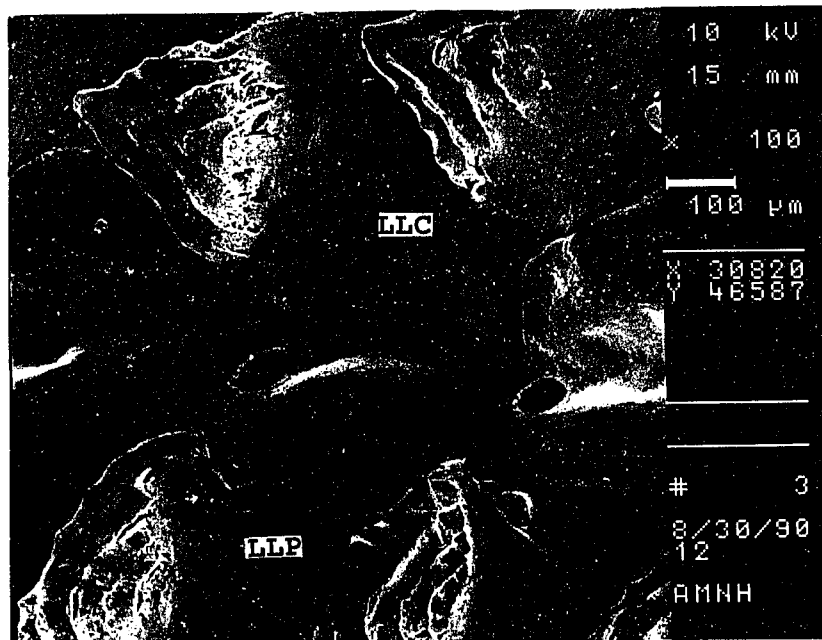


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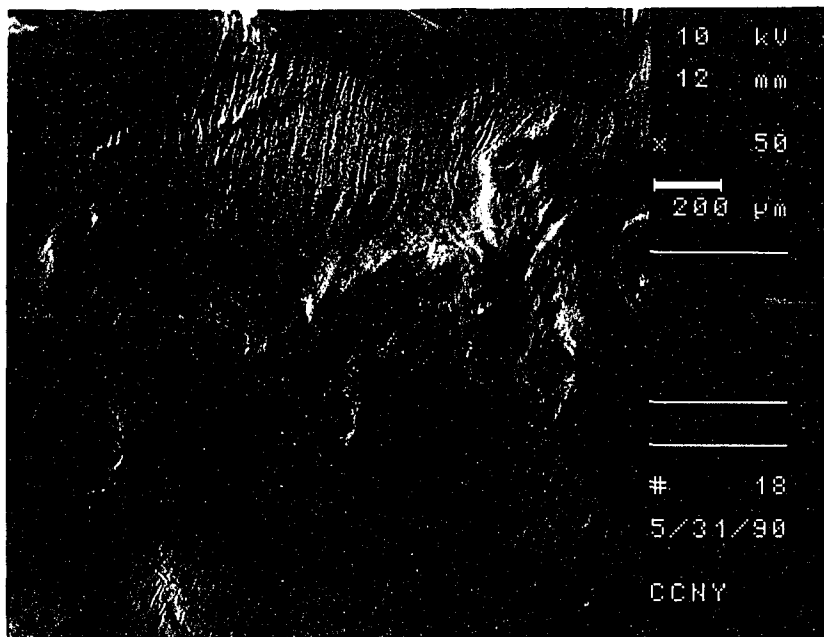


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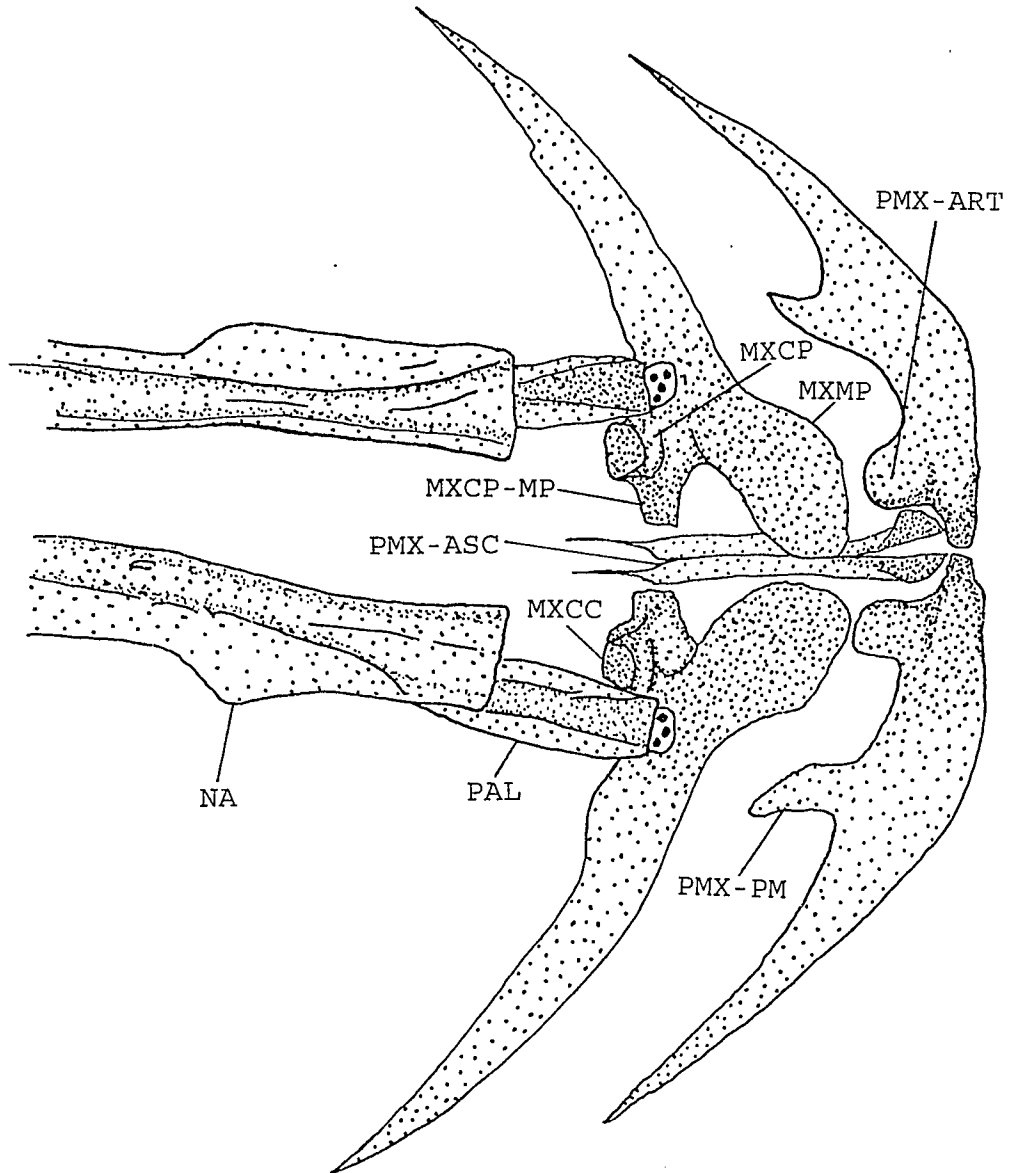


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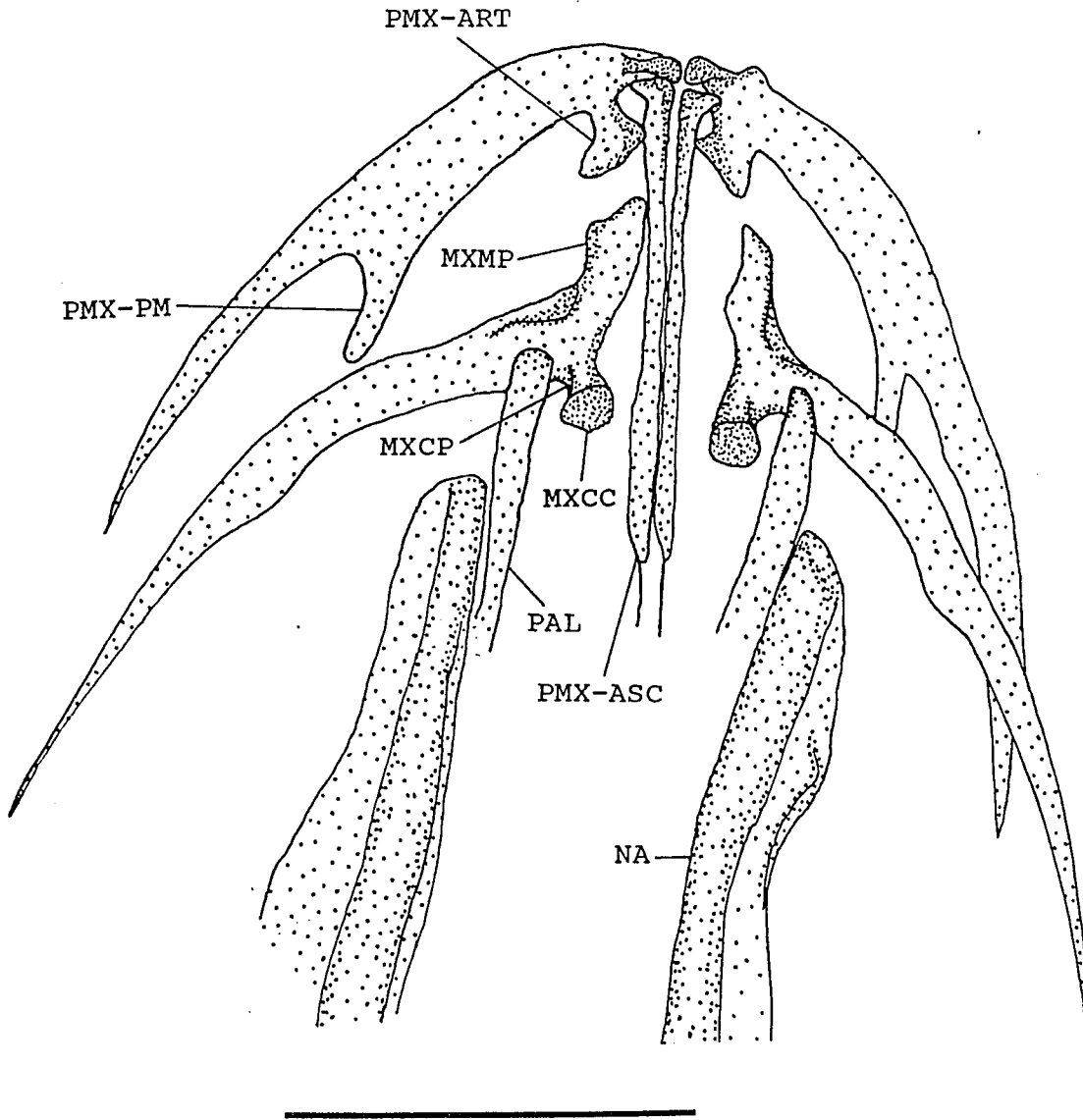


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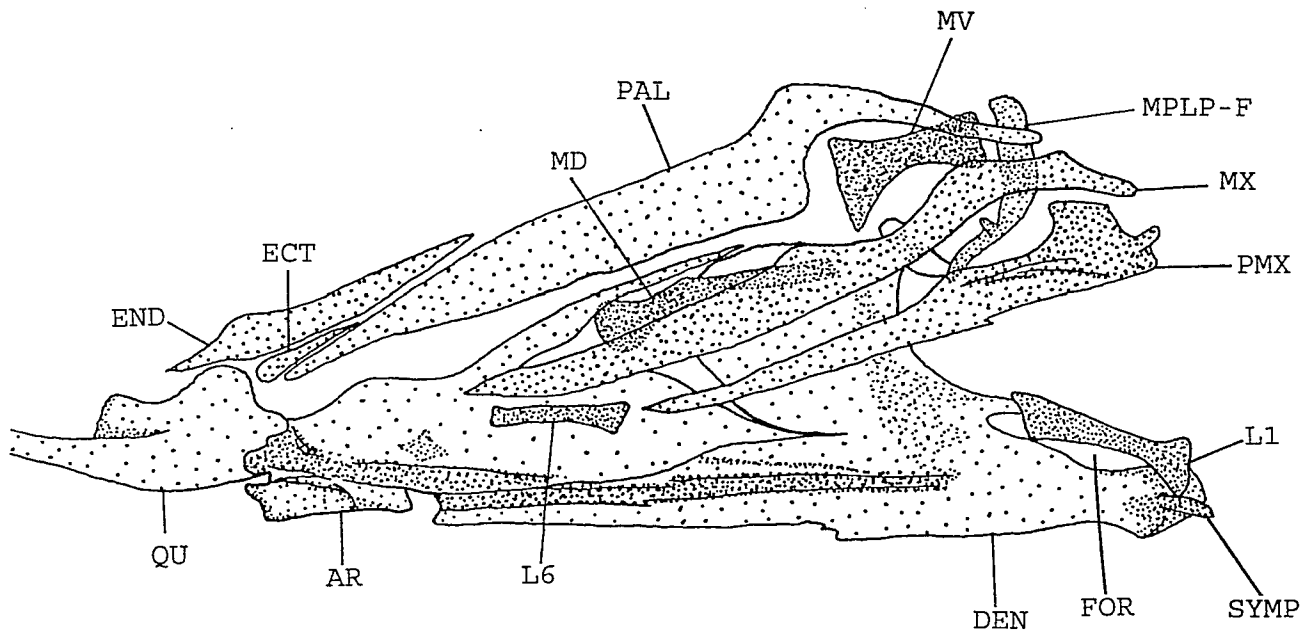


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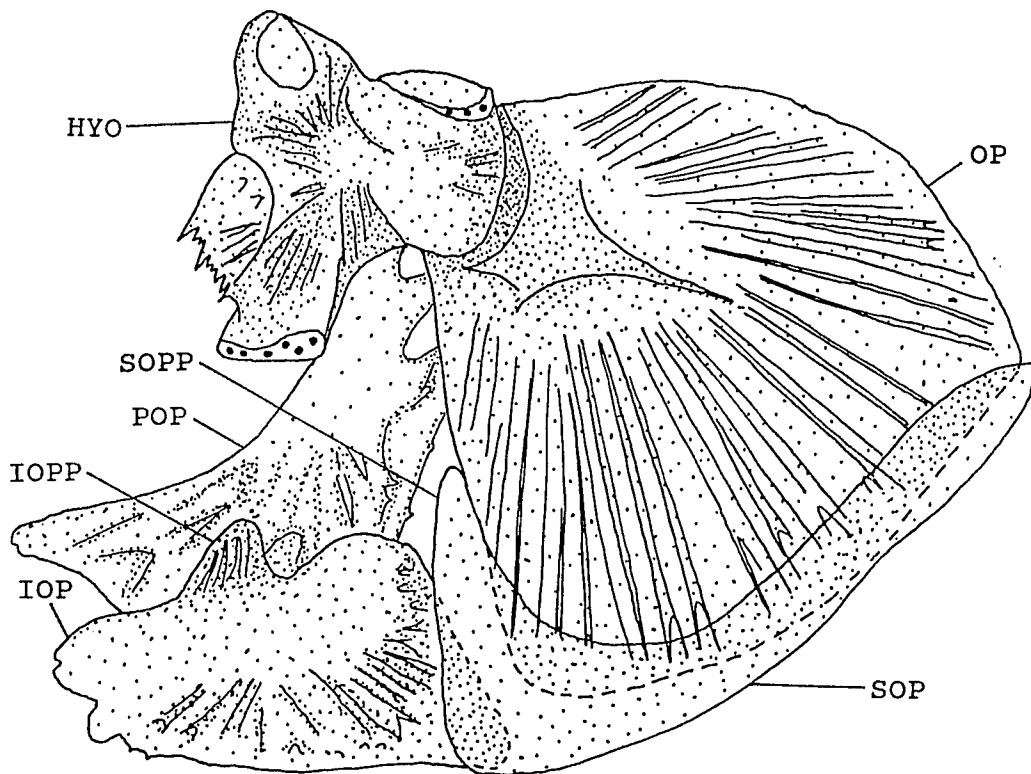


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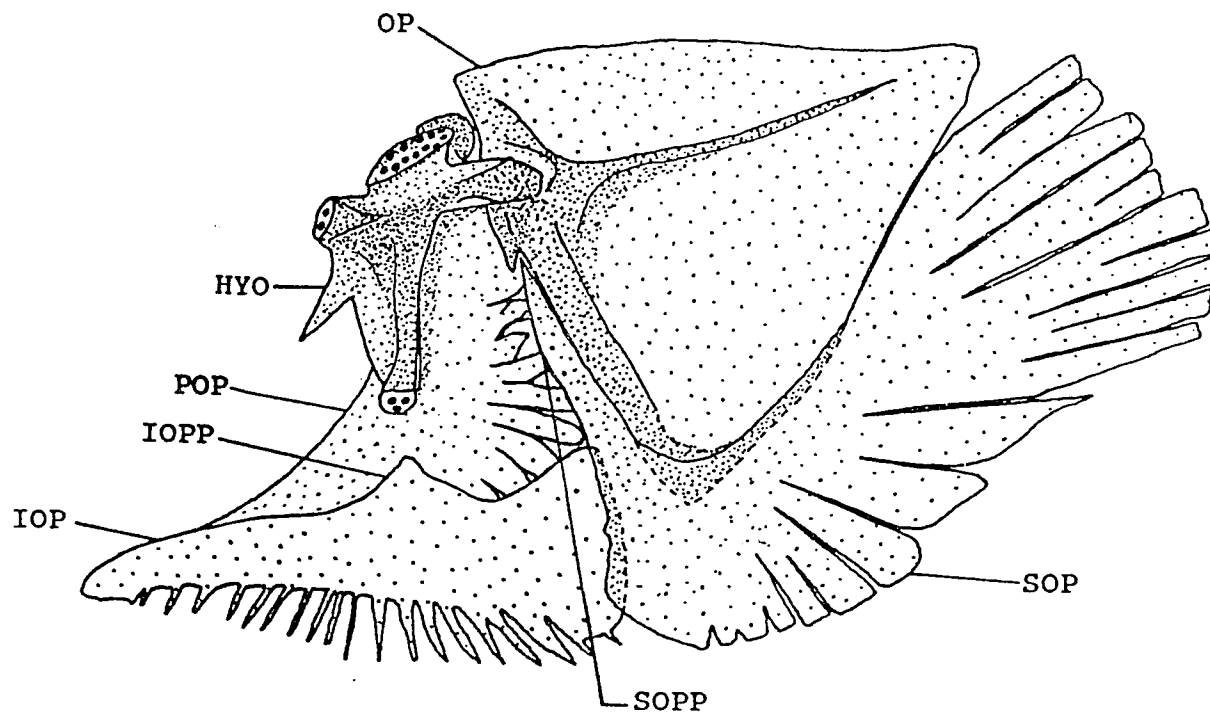


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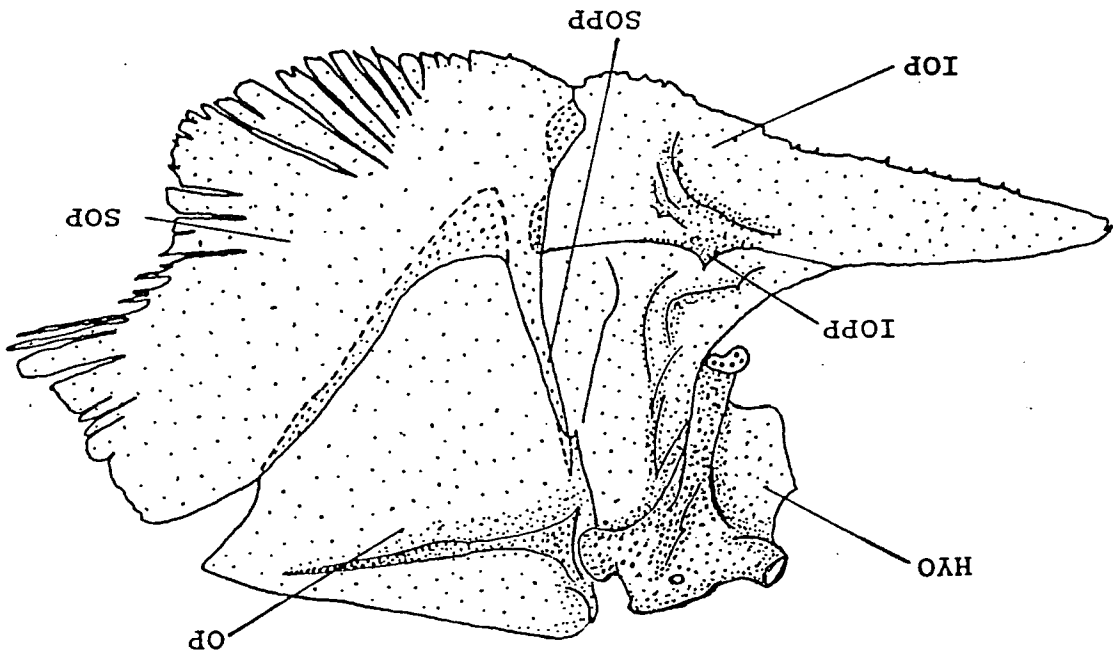


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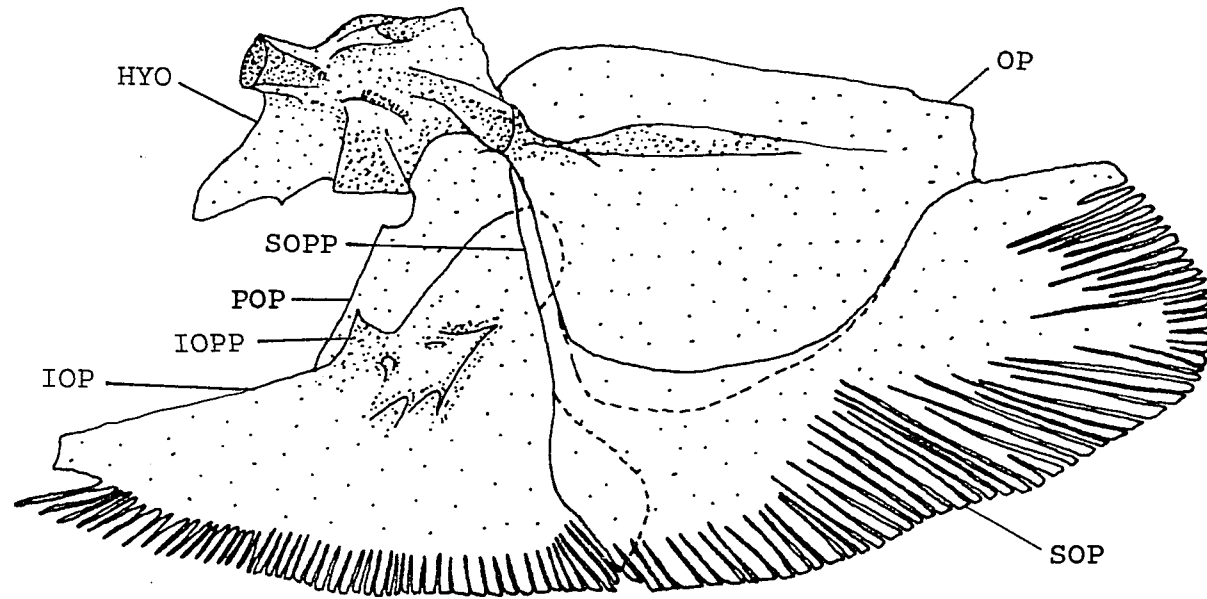


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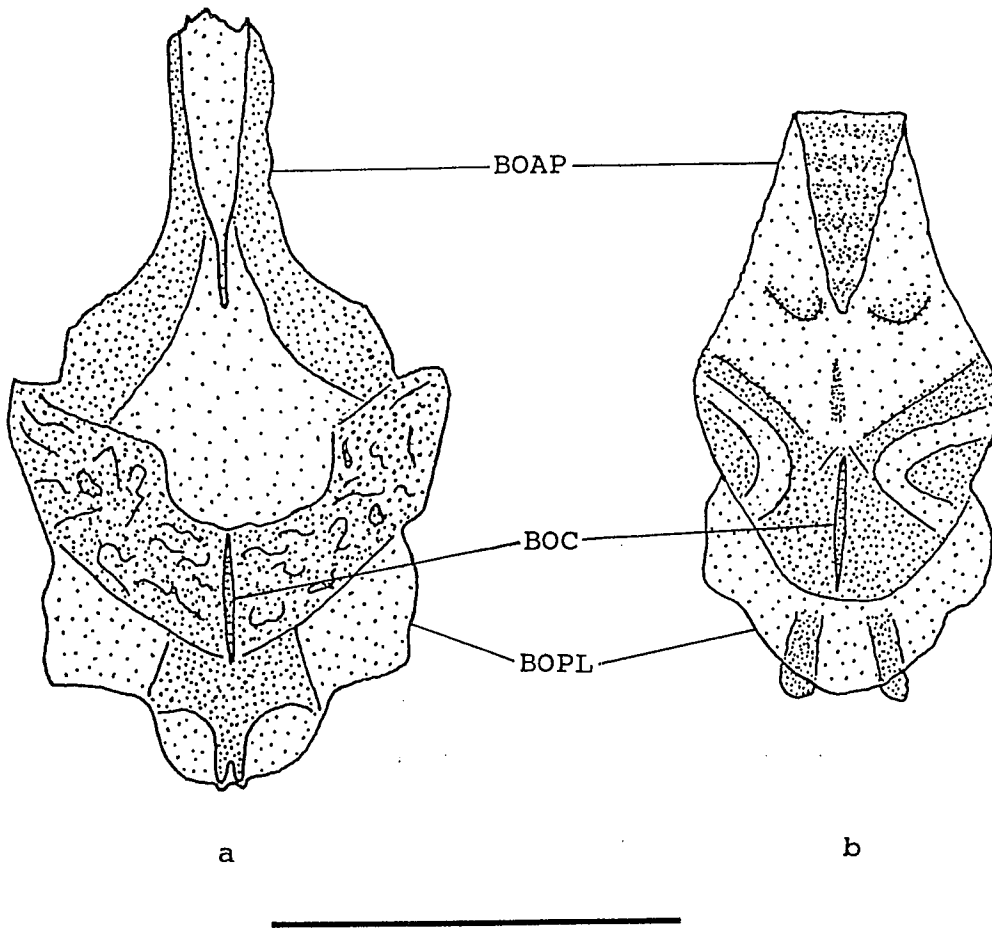


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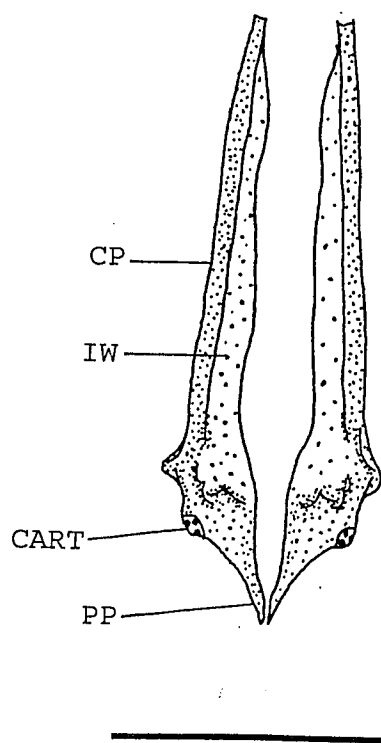


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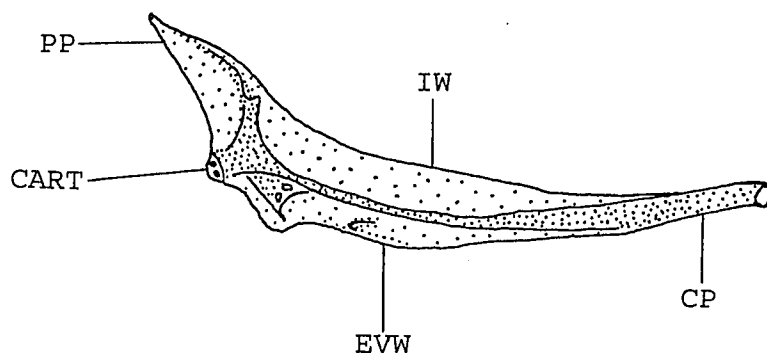


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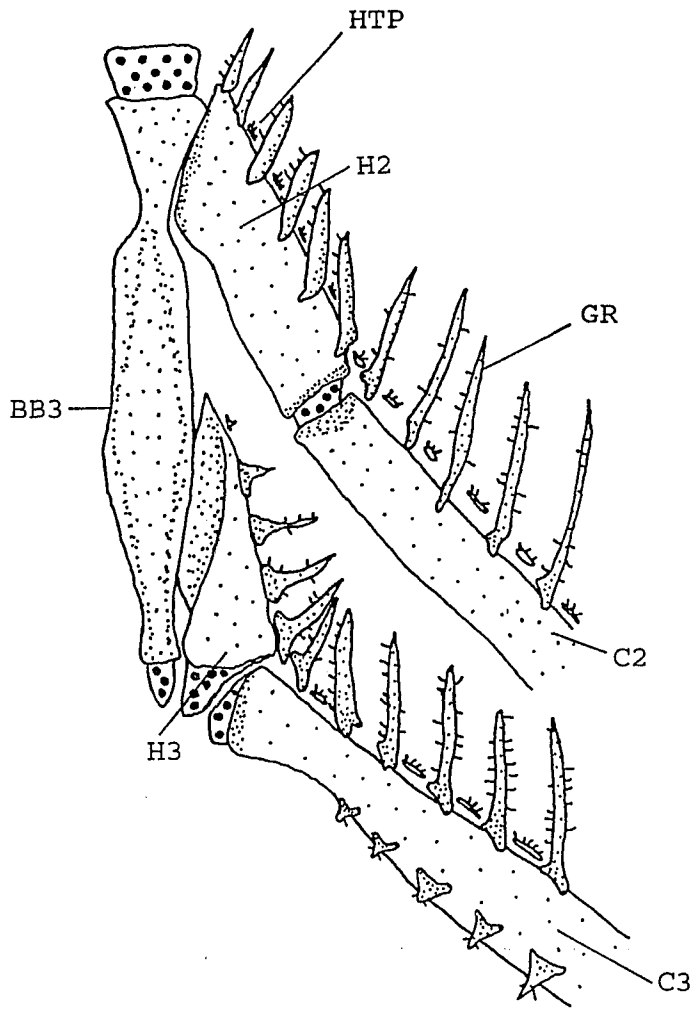
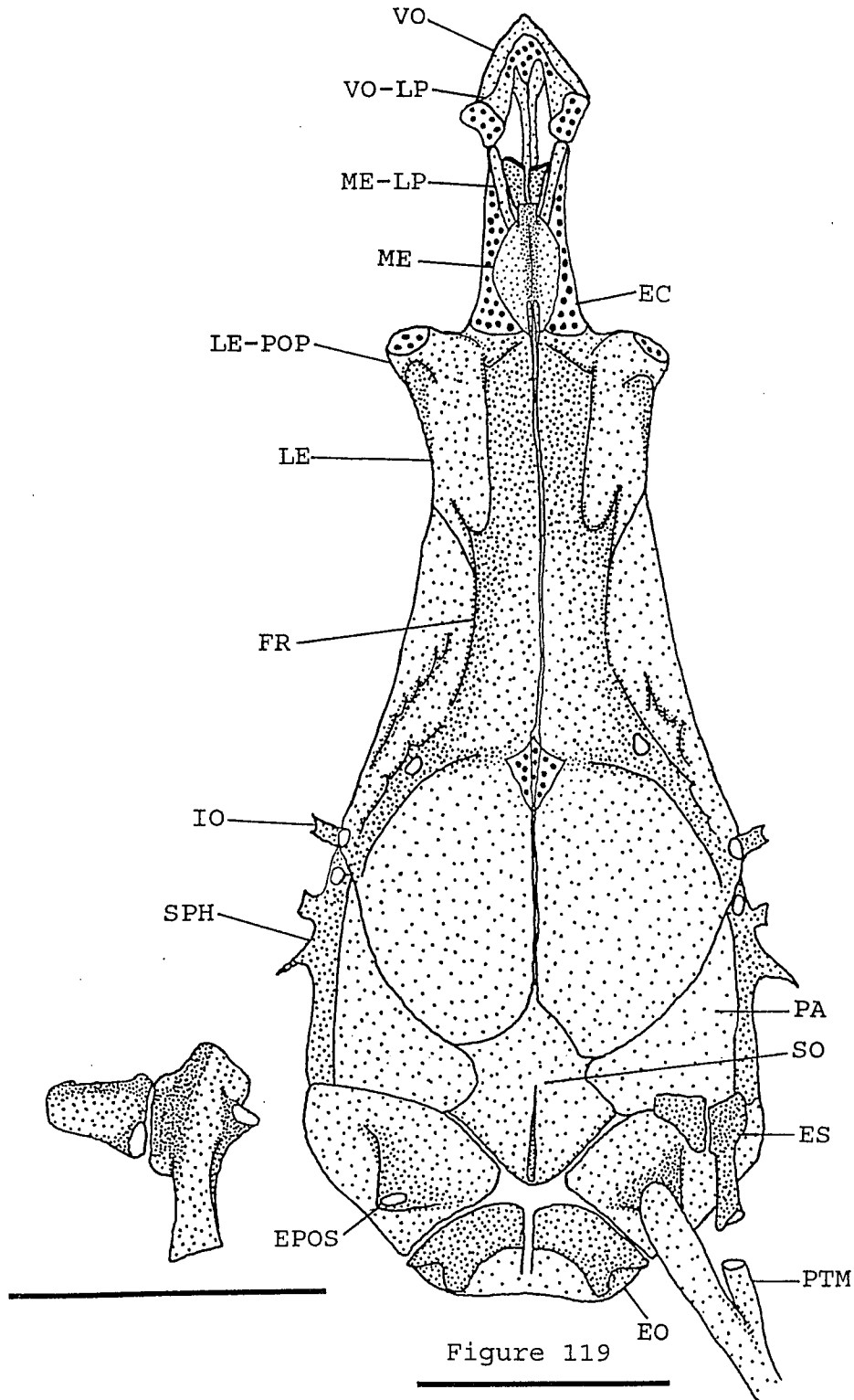


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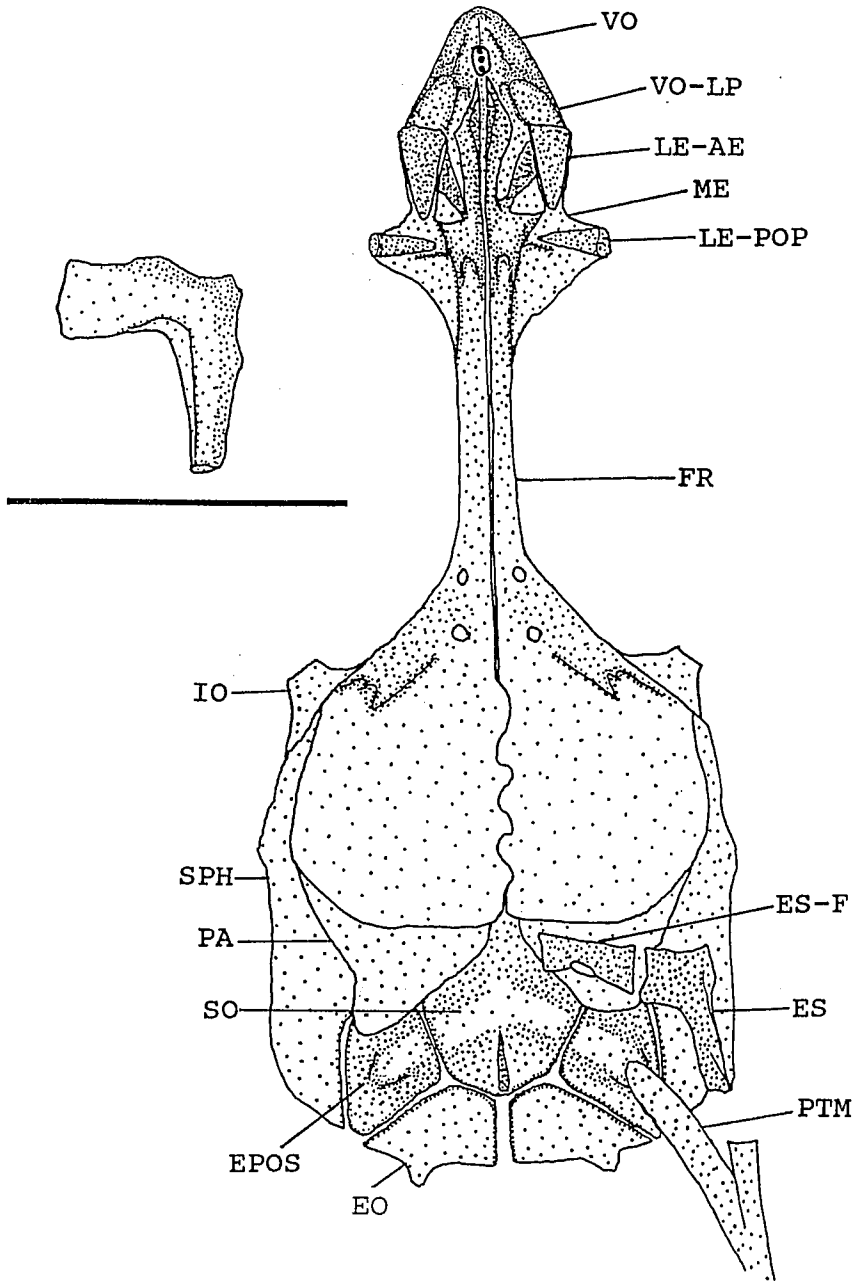


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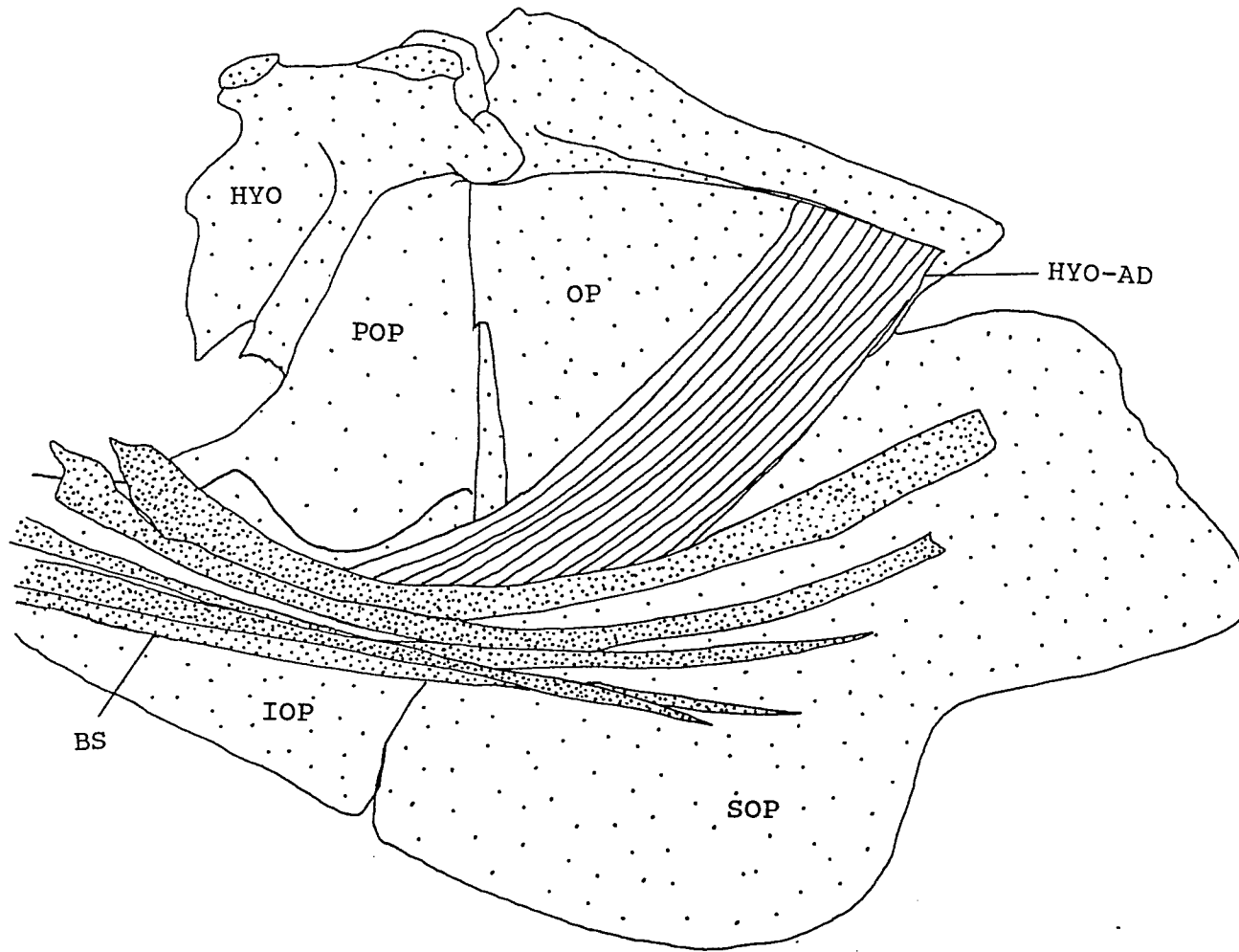


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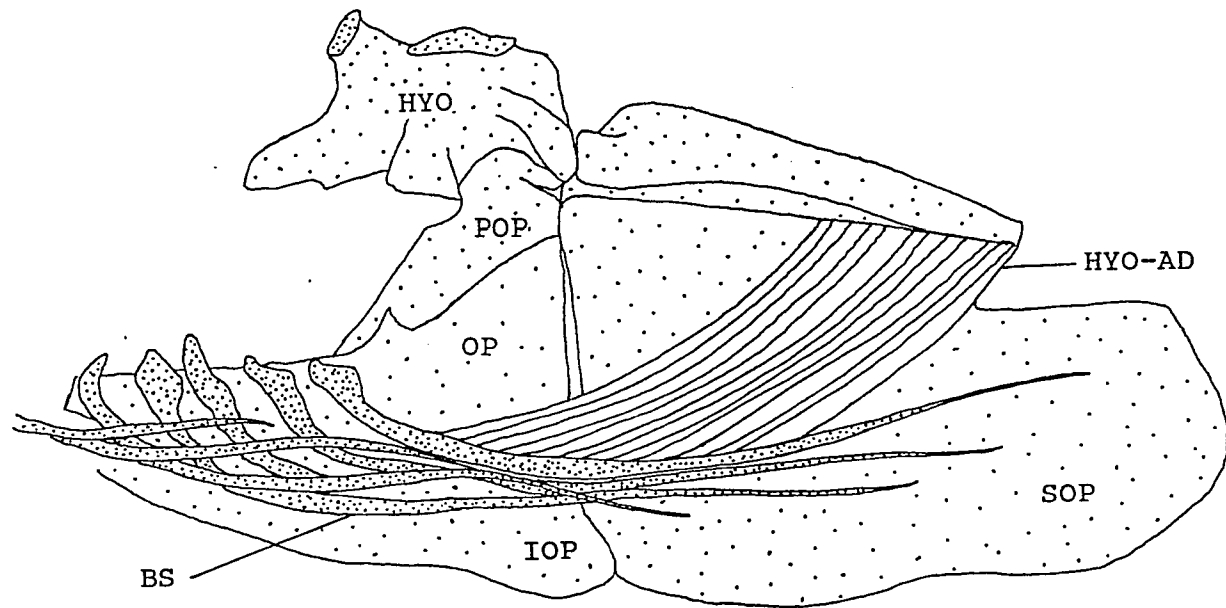


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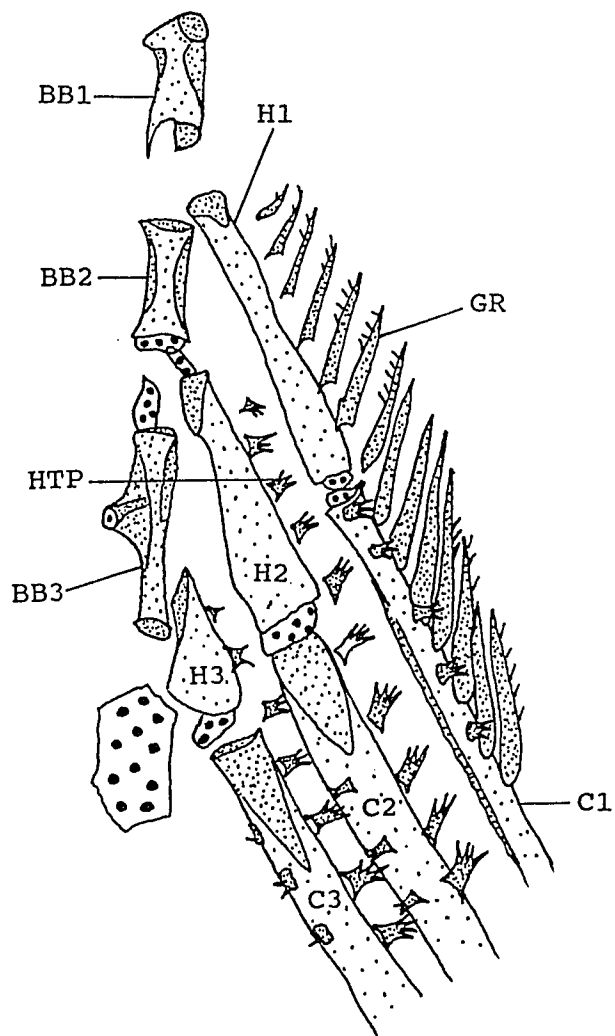


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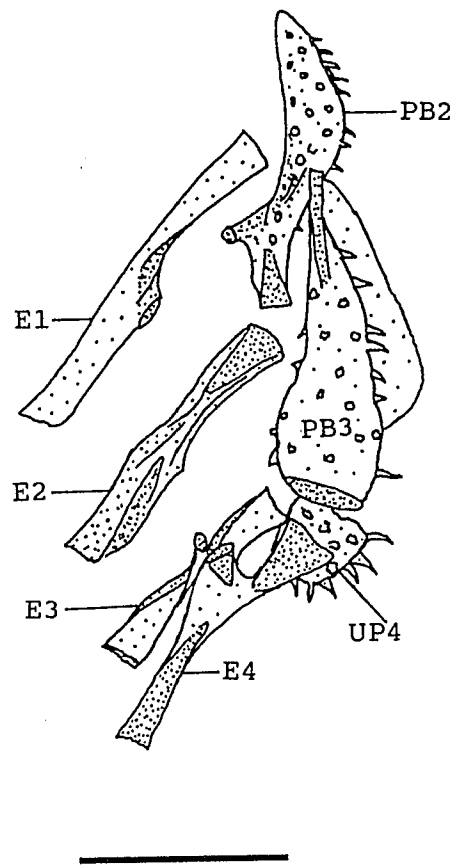


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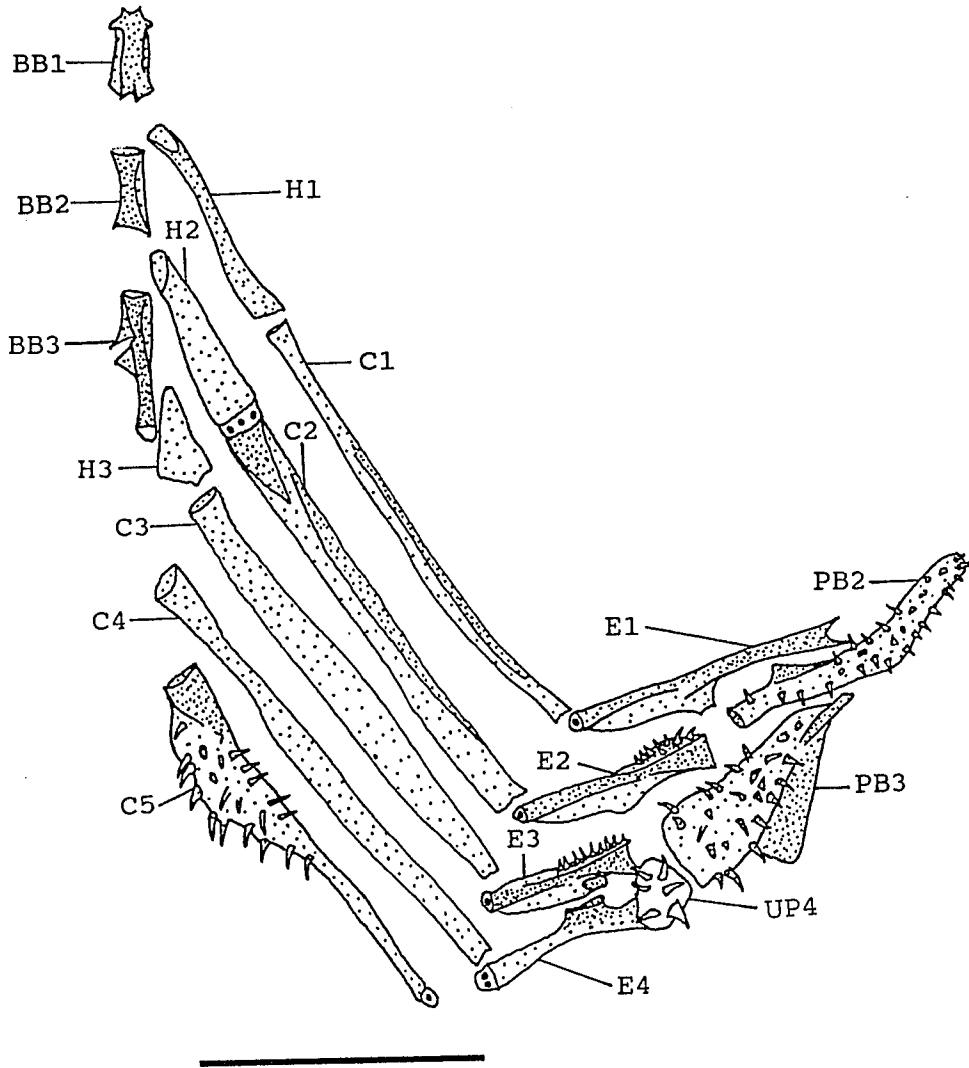


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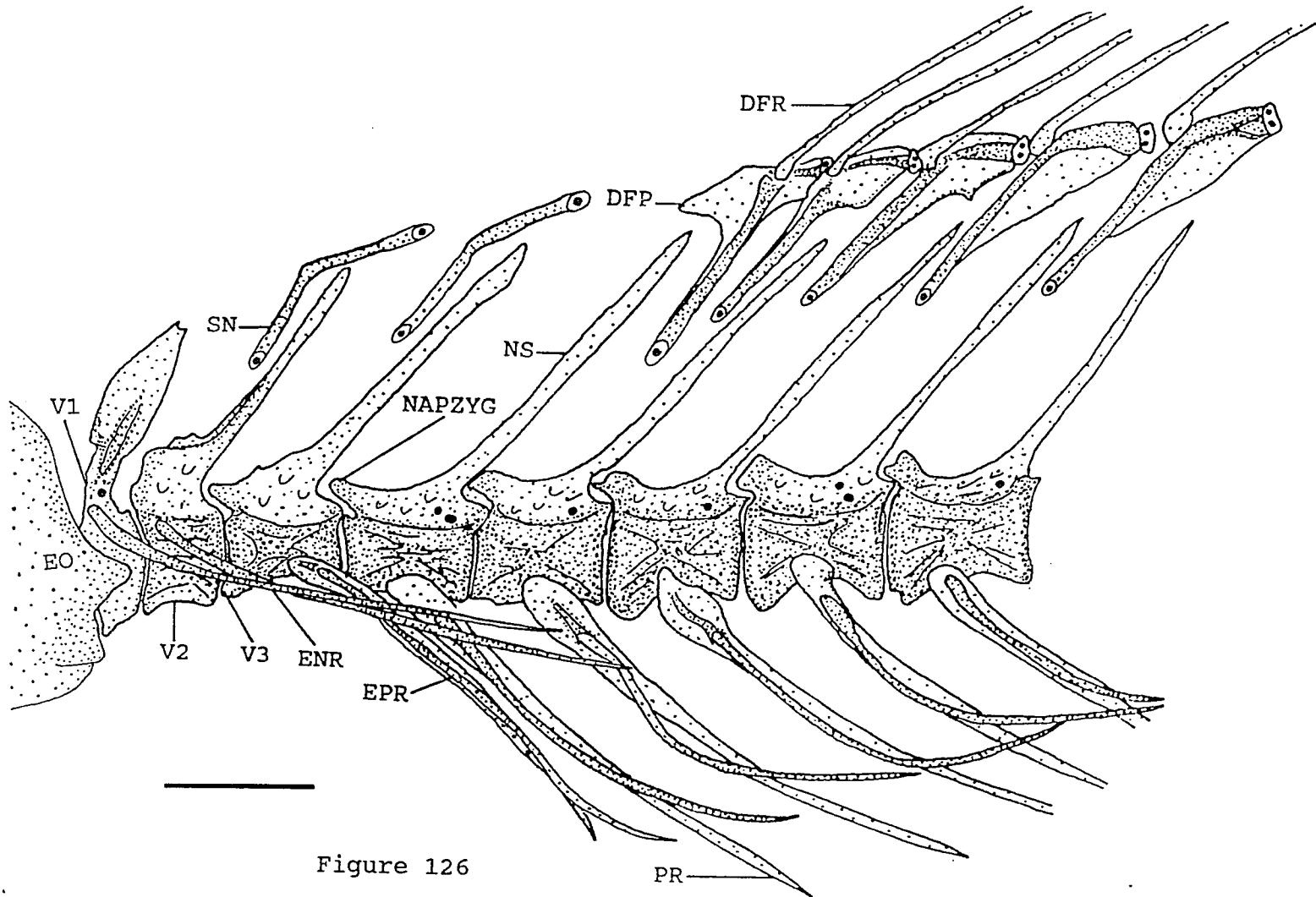


Figure 126

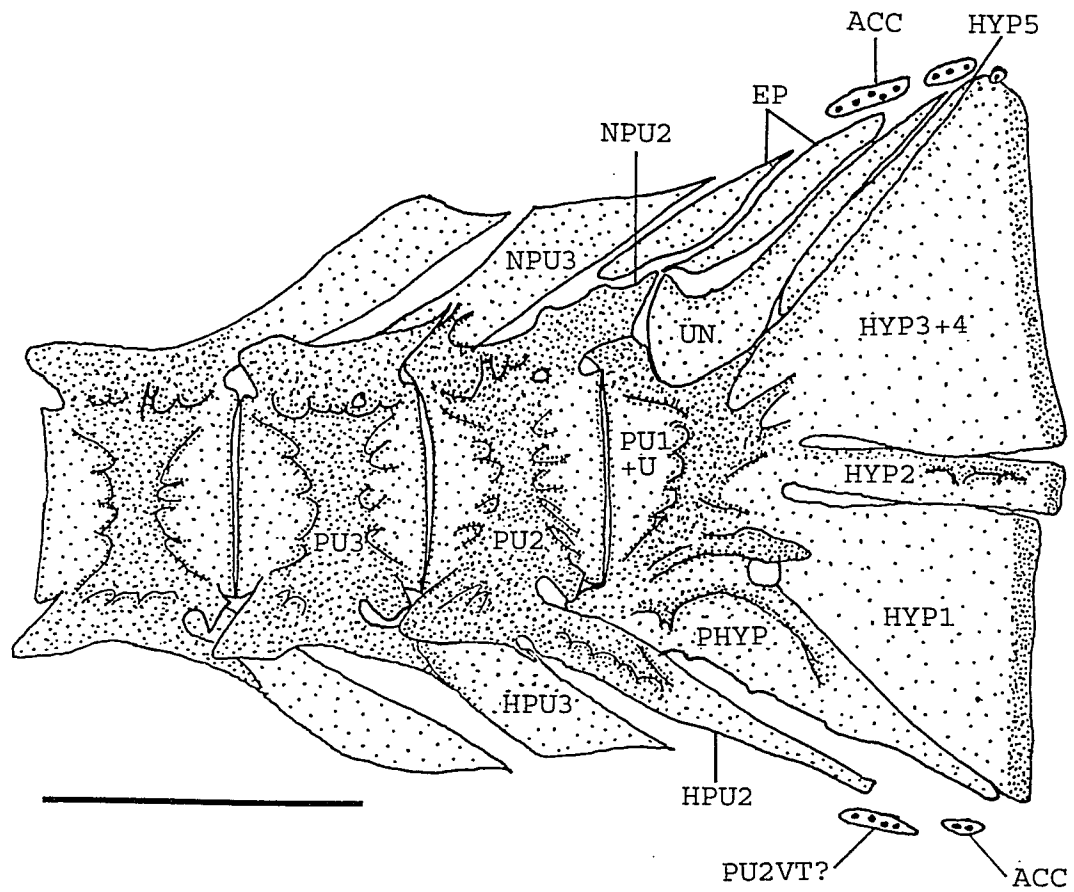


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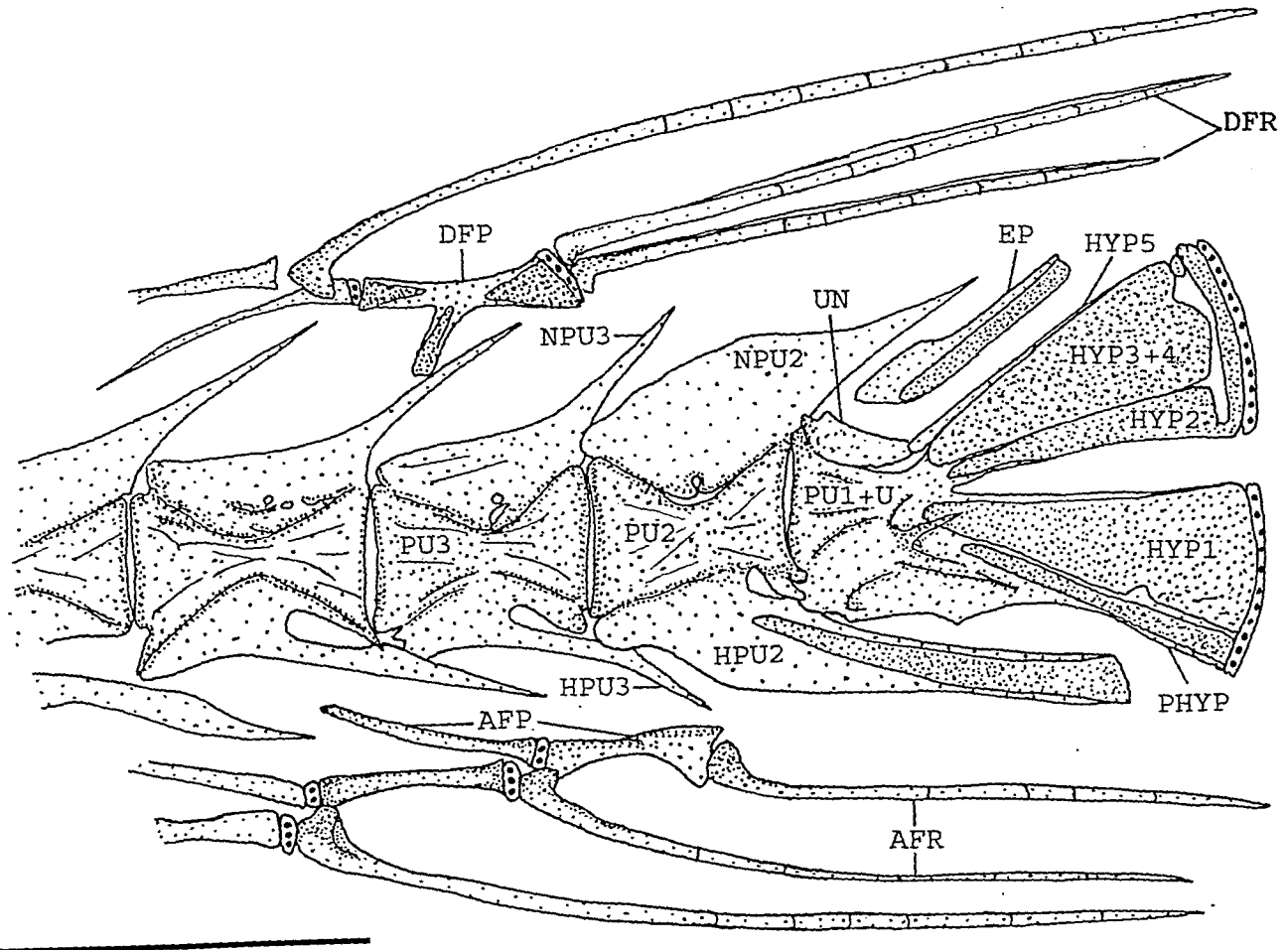


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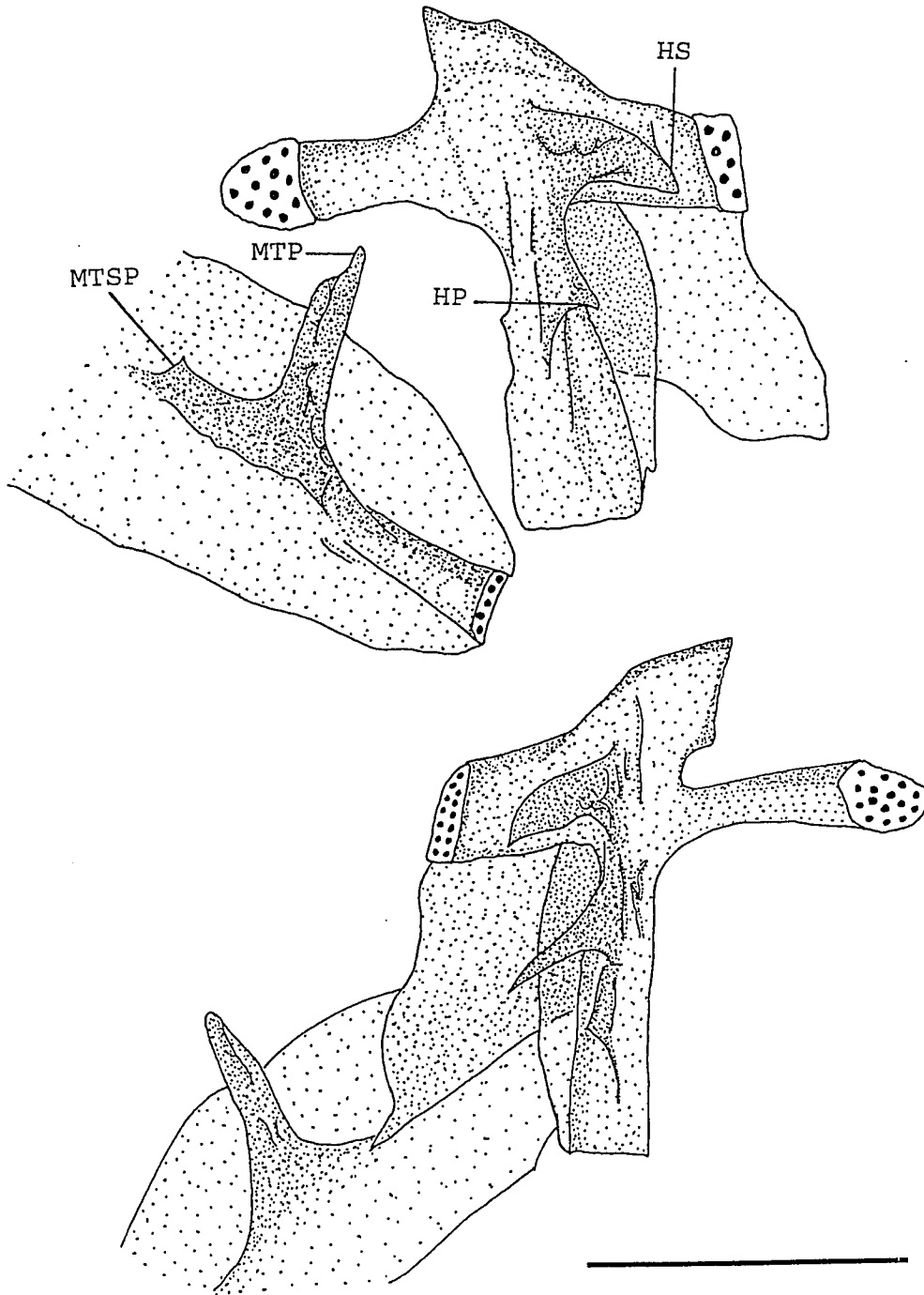


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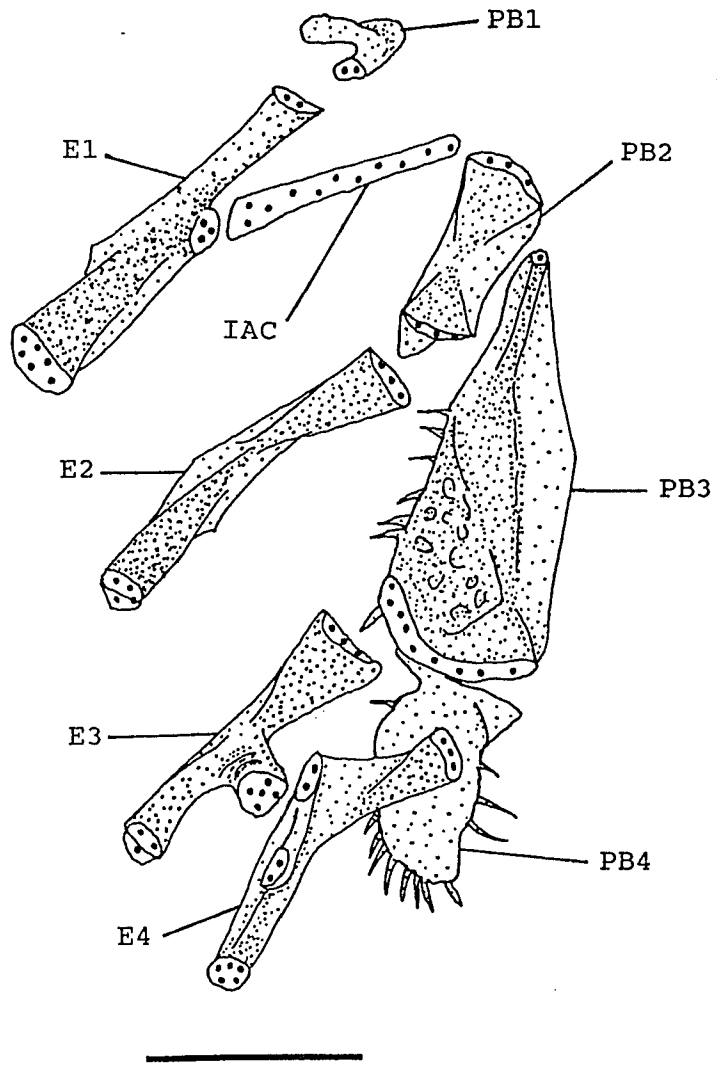


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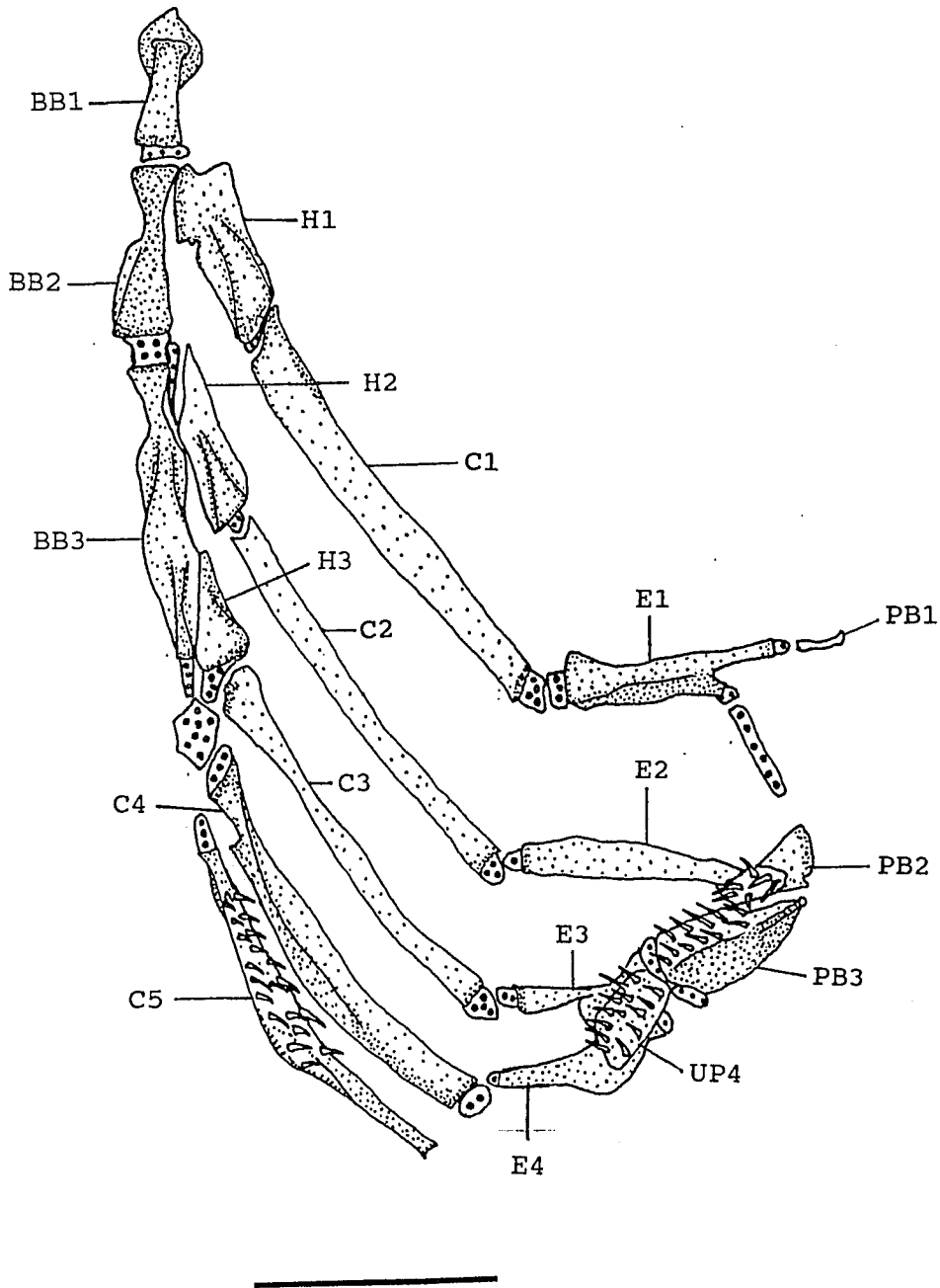


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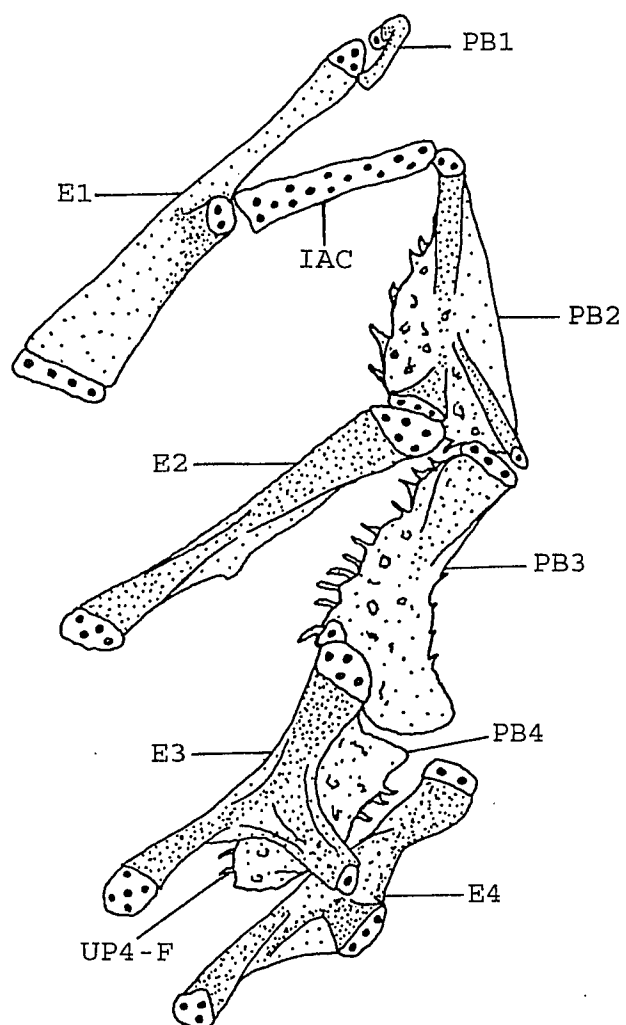


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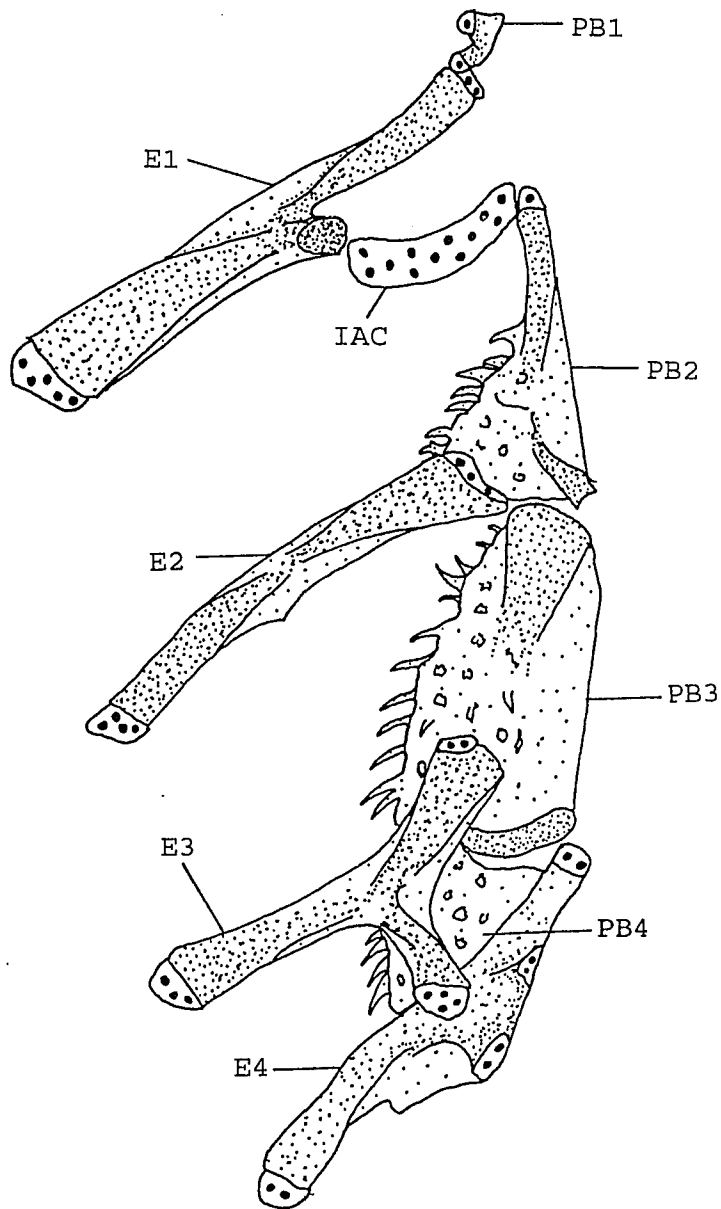


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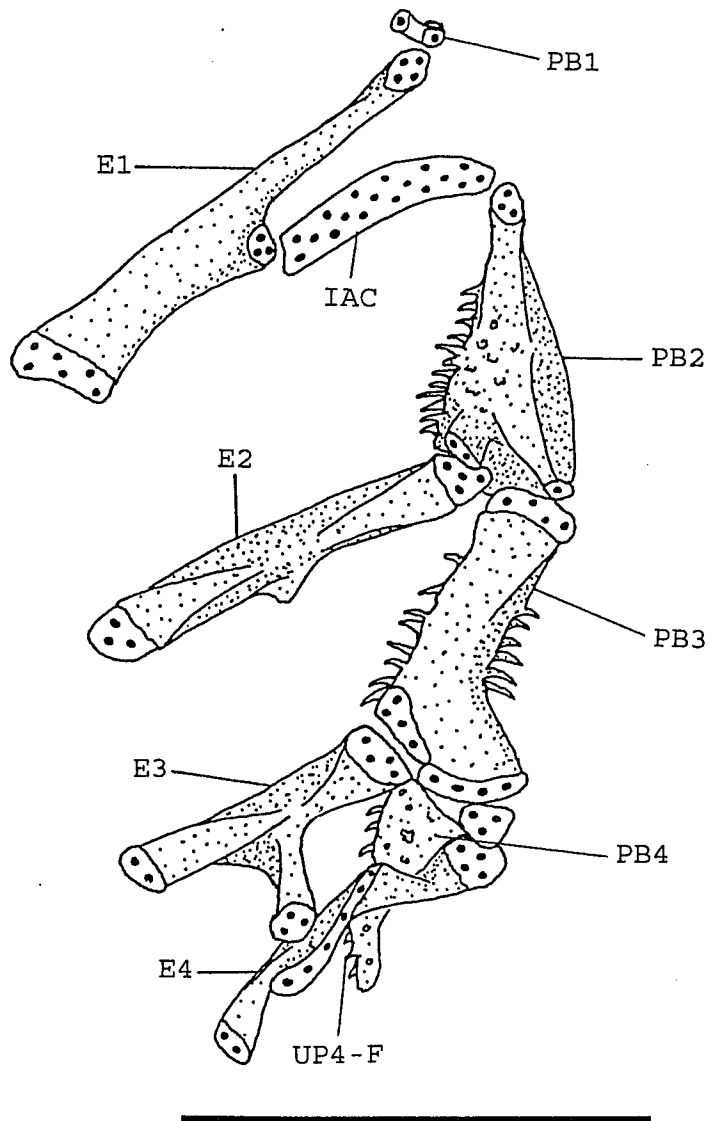


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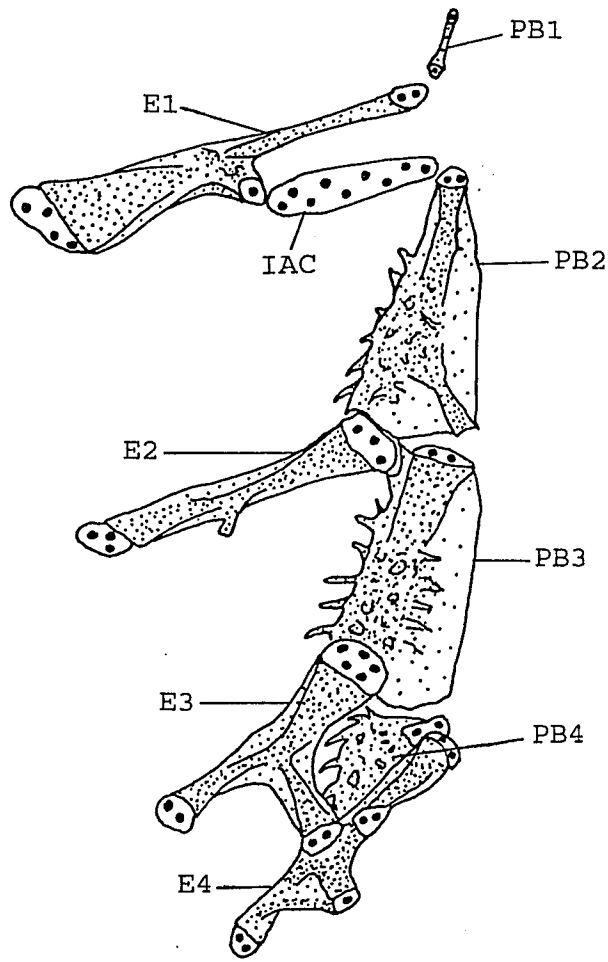


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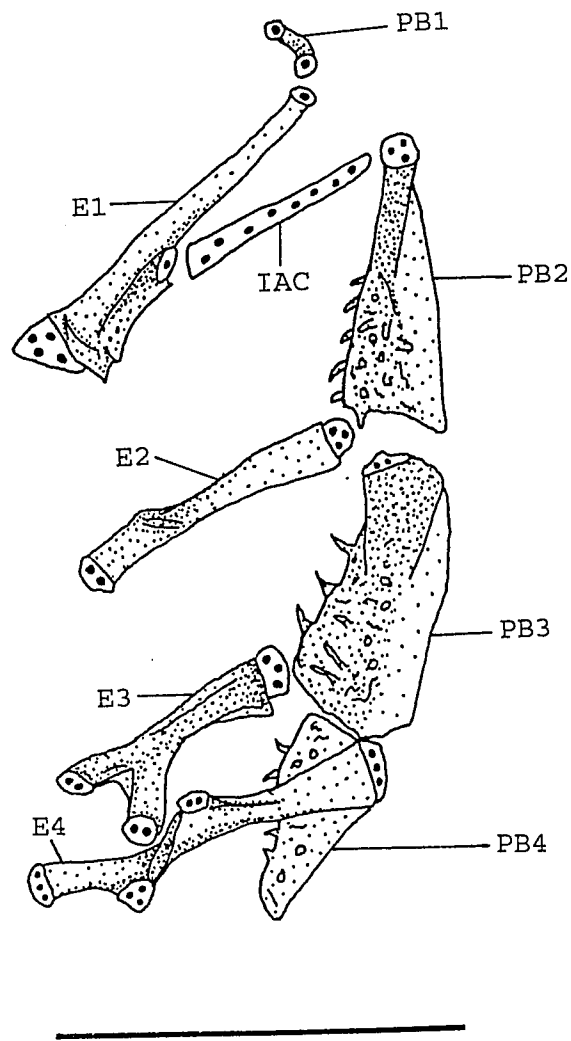


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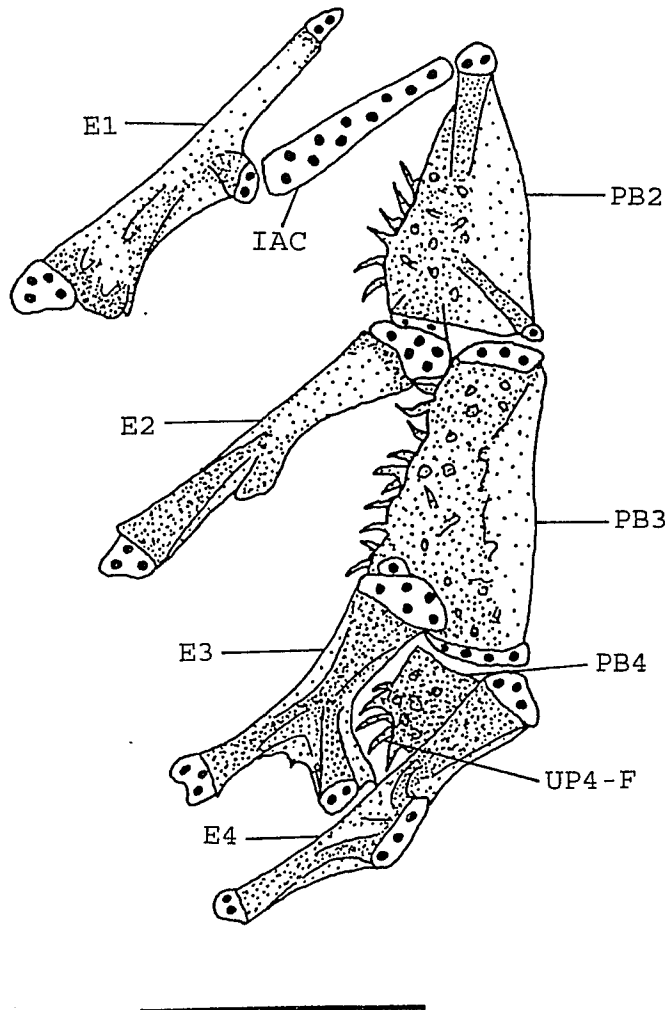


Figure 137

Figure 138

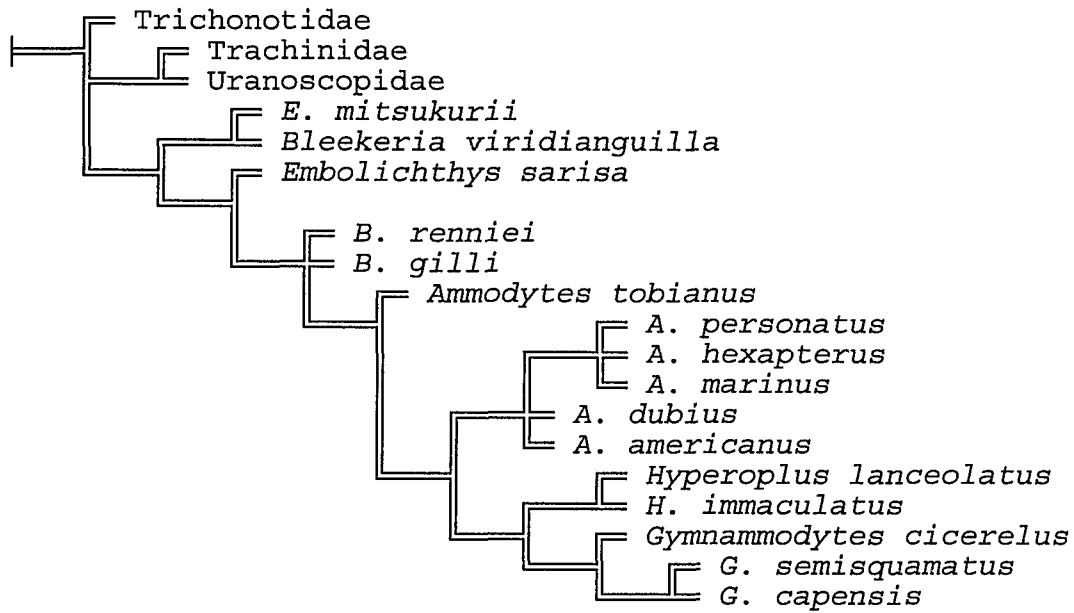
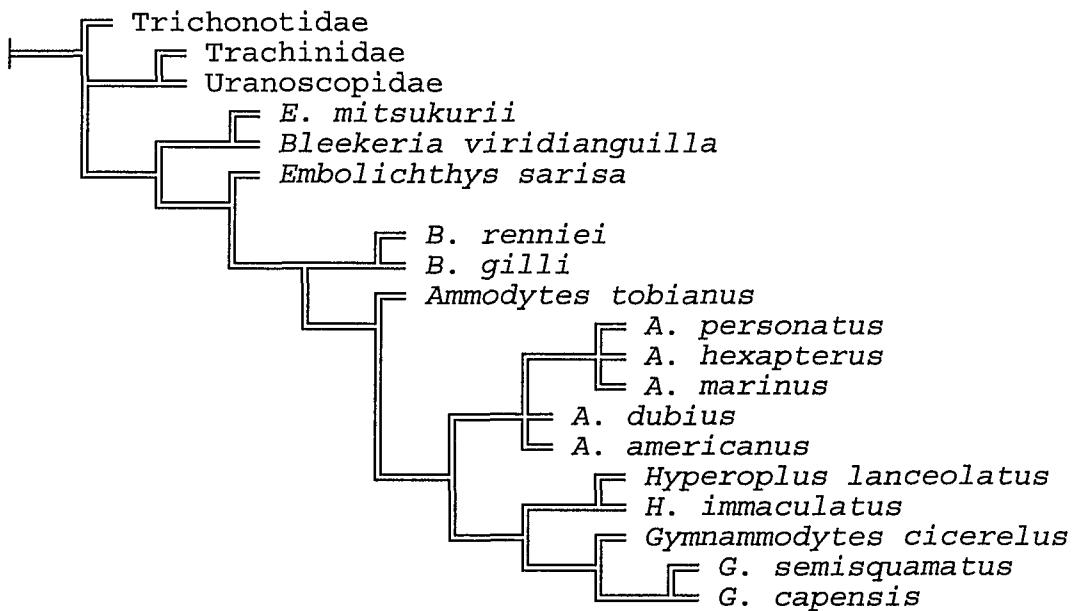


Figure 139



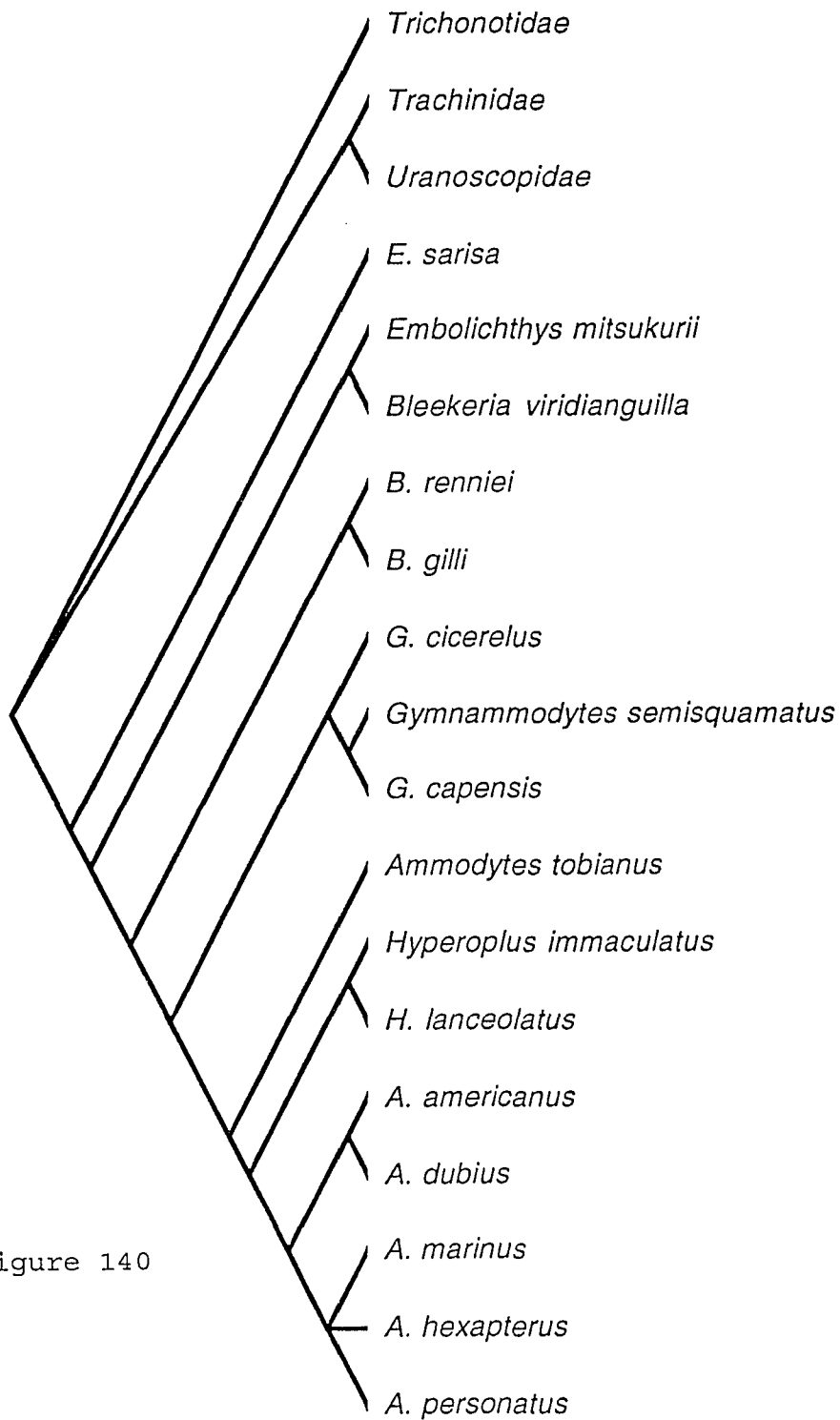


Figure 140

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