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Comparative Morphology of the Fishes of the Family Ammodytidae, with a Description of Two New Genera and Two New Species

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Hitoshi Ida, Pailoj Sirimontaporn and Supap Monkolprasit (1994) Comparative morphology of the fishes of the family Ammodytidae, with a description of two new genera and two new species. *Zoological Studies* **33**(4): 251-277. The generic characters of the fishes of the family Ammodytidae are discussed and two new genera and two new species are described.

The new genus *Protammodytes* (type species: *Protammodytes brachistos*) is characterized by the presence of pelvic fins and a symmetric squamation, fewer vertebrate, and a complete series of infraorbitals. These characters are believed to be least derived state among the family Ammodytidae. Another new genus *Lepidammodytes* (type species: *Lepidammodytes macrophthalmus*) is characterized by having strongly ctenoid scales, larger eyes, perforated lacrymals, and a moderate number of vertebrae. The combination of general and derived characters is unique among the family.

The fishes placed in the genus *Bleekeria* Gunther are divided into two genera, *Bleekeria* and *Ammodytoides*. The genus *Bleekeria* includes *B. kallolepis, B. mitsukurii*, and *B. viridianguilla*. The genus *Ammodytoides* is comprised of *A. gilli, A. vagus, A. renniei, A. lucasanus, A. kimurai*, and *A. pylei*.

Embolichthys is moved to subgeneric level under the genus *Bleekeria*.

The seven genera of the family are grouped into two subfamilies, Bleekeriinae and Ammodytinae. The subfamily Bleekeriinae consists of *Protammodytes, Bleekeria, Lepidammodytes*, and *Ammodytoides*, the subfamily Ammodytinae consists of *Gymammodytes, Ammodytes*, and *Hyperoplus*. The Bleekeriinae share many general features. Ammodytinae is characterized by many derived features. Genera characters of *Ammodytoides* and *Gymnammodytes* fill the gap between the generalized and specialized subfamilies.

Key words: Ammodytidae, Morphology, *Protammodytes* (gen. nov.), *Lepidammodytes* (gen. nov.).

The ammodytid fishes are characterized by an elongated body, reduced pelvic fins, a reduction of the number of principal caudal rays and branched dorsal and anal fin rays, as well as a greater number of abdominal vertebrae than caudal vertebrae. Combination of these characters presents an unique feature in the order Perciformes.

Fishes of the genera *Ammodytes* and *Hyperoplus* are distributed circumboreally, while less specialized forms such as *Bleekeria* sp. are found in tropical or temperate waters. A more primitive form was reported from the western tropical Atlantic (Robins and Bohlke 1970). The monotypic family Hypoptychidae, which had been regarded as the most specialized form among Ammodytoidei, was moved from the Perciformes to the Gasterosteiformes (Ida 1976).

Hitherto the ammodytids have been divided into two groups, viz. Ammodytinae and Bleekeriinae. These two groups were often assigned family status. Despite the smallness of the group, the relationships and their classification are still ambiguous because primitive form rarity and scarce comparative morphology imformation as well as other

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biological aspects of the members in the whole group. Recently, Pietsch and Zabetian (1990) presented clarified and detailed osteology of *Embolichthys mitsukurii* with special reference to family interrelationships and concluded that the family is a sister group of the families Trachinidae and Uranoscopidae, clarifying family placement. The present study aims to clarify the relationships between generalized warm water ammodytids and more specialized cold water forms.

MATERIALS AND METHODS

Materials used in the present study are listed below. *Ammodytoides gilli* and *A. renniei* were examined only by X-ray photographs. The following are institutional abbreviations. AMS: Australian Museum, Sydney, ANSP: Academy of Natural Sciences of Philadelphia, BPBM: Bernice P. Bishop Museum, BMNH: British Museum Natural History, FRSH: Fisheries Research Station, Hong Kong, FSFL: Far Seas Fisheries Laboratory, FSKU: School of Fishery Sciences Kitasato University, IMP: Izu Marine Park, KUFM: Museum of Fisheries, Kasetsart University, MFLB: Marine Fisheries Laboratory of Bangkok, NICA: National Institute of Coastal Aquaculture, Thailand, NSM: National Museum, Singapore, NSMT: National Science Museum, Tokyo, RUSI: J. L. B. Smith Institute of Ichthyology, Rhodes University, UCDZ: Department of Zoology, University of California, Los Angeles, USNM: National Museum of Natural History, Washington, D. C., ZUMT: Zoological Department, University Museum, University of Tokyo.

Protammodytes brachistos sp. nov.

Please see description of this species in page 254.

Protammodytes sarisa (Robins and Bohlke 1970)

Holotype, ANSP 1113091, 99.2 mm SL; paratype, ANSP 113092, 116.5 mm SL, off east of St. Vincent, Lesser Antilles.

Bleekeria kallolepis Gunther, 1862

Holotype BMNH, 103 mm SL, Madras. NICA 1161, 106 mm SL, Torutua National Park, Andaman Sea, Thailand.

Bleekeria mitsukurii Jordan and Evermann, 1902

FRSH 7111317, 6 individuals, 88-138 mm SL, Hong Kong. NSM 535, 1 individual, 115 mm SL, Malacca Strait. IMP 131-137, 7 individuals, 102-116 mm SL, Sagami Bay, Hajime Masuda. FSKU 810429, 17 individuals, 126-139 mm SL, Sagami Bay, Atsushi Ono. FSKU 70526, 13 individuals, 65-121 mm SL, Pescadores (Peng-Hu), Taiwan, Fish Market.

B. viridianguilla (Fowler, 1931)

KUFM 1307, 2 individuals, 93-96 mm SL, Gulf of Thailand. MFLB uncatalogued, 3 individuals, 103-111 mm SL. ZUMT 53973, 14 individuals, 96-146 mm SL, Pescadores (Peng-Hu), Taiwan, Fish Market. FSKU 74324 19 individuals, 112-133 mm SL, Malacca Strait.

Lepidammodytes macrophthalmus sp. nov.

Please see description of this species in page 255.

Ammodytoides gilli (Bean, 1895)

ANSP 45384, syntypes, 8 individuals, 83-116 mm SL. Collection data lost, supposed to be from eastern Pacific (Randall et al. 1993)

A. kimurai Ida and Randall, 1993

Holotype, NSMT-P 50708, 101 mm SL, Ogasawara Islands, off Minami-shima. Paratypes, BPBM 35421, 114 mm SL, FSKU 920601 3: 99-116 mm SL, all collected with the holotype.

A. lucasanus (Beebe and Tee-Van, 1938)

UCDZ W61-34, 3 individuals, 64-117 mm SL, Isla Ceralbo, close to the type locality.

A. pylei Randall, Ida and Earle, 1994

Holotype, BPBM 24868, 142 mm SL, Hawaiian Islands. Paratypes, BPBM 24868, 4:130-141 mm SL, Hawaiian Islands; FSKU 730318, 4 individuals, 159-173 mm SL. Collected by trawl net, operated at a sea mount 28°34'N, 176°42'7W, west off Midway Island, depth of 77 m, by R/V Kaiyo Maru, March 18, 1973.

A. renniei (Smith, 1957)

RUSI 174, 55.9 mm SL; RUSI 674, 60 mm SL (paratype).

A. vagus (McCulloch and Waite, 1916)

AMS I-9272. Holotype, 150 mm SL, Lord Howe Island. AMS I-B 3241, 54.5 mm SL, New South Wales.

Gymnammodytes capensis (Barnard, 1927)

FSFL N-715, 11 individuals, 141-180 mm SL, Ivory Coast.

G. cicerelus (Rafinesque, 1810)

FSKU 78520, 32 individuals, 94-121 mm SL. Messina Fish Market, Sicily.

G. semisquamatus (Jourdain, 1879)

USNM 108813, 2 individuals, 168-170 mm SL. 57°38'N, 8°33'W (British Islands).

Ammodytes hexapterus Pallas, 1831

FSKU 70715, 8 individuals, 95-116 mm SL. Bristol Bay as stomach content of a *Paralichthys stellatus*. FSKU 73509, 37 individuals, 137-174 mm SL. Bristol Bay.

A. marinus Raitt, 1934

FSKU 781012, 6 individuals, 145-167 mm SL, North Sea, 45°10'N, 8°07'E.

A. personatus Girard, 1859

FSKU 70422, 58 individuals, 22-130 mm SL. Hiratsuka, Sagami Bay, by beach seine. FSKU 71410, 10 individuals, 142-149 mm SL. Tsukiji Fish Market.

A. tobianus Linnaeus, 1758

FSKU 781011, 5 individuals, 156-171 mm SL, North Sea, 45°10'N, 8°07'E.

Hyperoplus lanceolatus (Sauvage, 1824)

FSKU 73912, 6 individuals, 216-258 mm SL, North Sea, 60°18'N, 2°35'E.

Osteological descriptions were based on the following specimens: *Protammodytes brachistos* (holotype 86 mm), *P. sarisa* (paratype, 116.5 mm), *Bleekeria mitsukurii* (118 mm), *B. viridianguilla* (112 mm), *B. kallolepis* (104 mm), *Ammodytoides lucasanus* (117 mm), *A. pylei* (166 mm), *A. vagus* (holotype 150 mm), *Gymnammodytes capensis* (147 mm), *G. cicerelus* (120 mm), *G. semisquamatus* (170 mm), *Ammodytes hexapterus* (116 mm), *A. personatus* (147 mm), *A. tobianus* (156 mm), *Hyperoplus lanceolatus* (252 mm). Excluding the holotype, specimens were cleared with trypsin and stained with alizarin red S. Drawings for the holotypes and vertebral counts were based on X-ray photographs. Caudal vertebrae were defined as those having closed haemal spines. Counts for fin rays, scales, gill rakers, and branchiostegals were made under a binocular microscope. Caudal concavity was defined as the horizontal distance between verticals at the tip of the longest and the shortest caudal-fin rays. Drawings were made by the authors with a camera lucida. Characters shared with less derived trachinoid fishes such as Pinguipedidae and Champsodontidae were regarded as generalized or primitive, and those derived from less derived trachinoids were regarded as specialized or advanced.

Key to Genera

1a. Pelvic fin present, length of the girdle more than 2.9% SL; scales not embedded in oblique dermal plicae, not arranged to form a diagonal straight line; lateral line scales less than 95; lateral line simple, without branch or accessory sensory villi just above lateral line ..... *Protammodytes*

1b. Pelvic fin present or absent, length of the girdle less than 2.0% SL; scales more or less embedded in oblique plicae (excluding *Gymnammodytes* in which scales are absent from most of the body), arranged to form a diagonal straight line; lateral line with branch or accessory sensory villi below dorsal fin; more than 100 lateral line scales 2

2a. Lateralis system of head continuous with that of body; ventral skin fold absent; rays of dorsal and anal fins branched; dorsal rays less than 50 (rarely 51) and anal rays less than 25; scales moderate, fewer than 120 on lateral line, less than 20 rows below lateral line; compressed caudal peduncle, longer than deep; fewer than 36 abdominal vertebrae 3

2b. Lateralis system on head discontinuous with that on body at posttemporal region; ventral skin fold present at least below pectoral; rays of dorsal and anal fins unbranched, more than 51 (rarely 50) dorsal rays and more than 26 anal rays; scales fine, more than 120 on lateral line, rows below lateral line more than 28 if present; cylindrical caudal peduncle, length about equal to depth;more than 37 abdominal vertebrae 4

3a. Teeth present on both jaws; continuous subocular canal, not interrupted below eye; deep caudal peduncle, about 1/3 HL; fewer than 18 anal fin rays; neural and haemal spines of posterior caudal vertebrae not expanded; 8 infraorbitals (including lachrymal); labial ossicles absent; eye medium, about 1/5 HL ..... *Bleekeria*

3b. Teeth absent from jaws; subocular canal interrupted below eye; low caudal peduncle, about 1/4 of HL; anal fin rays 18 or 19; neural and haemal spines of posterior caudal vertebrae not expanded; infraorbitals 8; labial ossicles absent; eye large, about 1/4 HL ..... *Lepidammodytes*

3c. Teeth absent from jaws; subocular canal interrupted below eye caudal peduncle low, less than 1/4 of HL; anal fin rays 21 to 25; neural and haemal spines of posterior vertebrae expanded; infraorbitals 6; labial ossicles present; eye small, less than 1/5 HL ..... *Ammodytoides*

4a. Scales absent from most of body; labial ossicles present lateral line branched, pores opening both above and below lateral line ..... *Gymnammodytes*

4b. Scales always present; labial ossicles absent; lateral line simple, without branch, pores open in a straight line, bearing accessory sensory villi below dorsal fin base 5

5a. Premaxillary protrusile; tip of prevomer straight, not protruded from roof of mouth ..... *Ammodytes*

5b. Premaxillary not protrusile; tip of prevomer curved downward, protruded from roof of mouth ..... *Hyperoplus*

Protammodytes gen. nov.

Type species: *Protammodytes brachistos*, new species.

Diagnosis: Distinguishable from all other genera within the family by the presence of a larger pelvic fin, its length is more than 5.9% SL, and larger scales are not arranged in diagonal straight lines. Less than 92 scales on lateral line. Neural and haemal spines of the caudal vertebrae not expanded. Complete and bold infraorbitals. Ventrolateral skin fold and plicae absent. Labial tissues

not ossified. Olfactory lamellae not reduced and situated throughout the entire nasal cavity.

Remarks: This new genus consists of two species, *Protammodytes brachistos* sp. nov. and *P. sarisa* (Robins and Bohlke 1970) formerly identified as *Embolichthys sarisa*.

Key to species of *Protammodytes*

1a. 36 or 37 dorsal rays; 16 or 17 anal rays; lateral line scales 92, scales above and below lateral line 4/13; pelvic fin more than 7% SL; body not slender, depth about 1/7 of standard length; procurrent caudal ray 15/16; central Pacific. ..... *P. brachistos* sp. nov.

1b. 43 to 45 dorsal rays; 17 anal rays; 92 to 95 lateral line scales, scales above and below lateral line 4/9; pelvic fin about 6% SL; body rather slender, depth about 1/10 of standard length; procurrent caudal ray 18/17; western Atlantic. ..... *P. sarisa*

Protammodytes brachistos sp. nov.

(Figs. 1, 3A, 4A, 5A, 9A, 10A, 12A, 13A, 14A; Table 1)

Holotype: FSKU 701117, 86 mm SL, from the stomach content of an *Etelis* sp., 500 g in body weight, angled at 24°07'N, 123°18'E, off east coast of Taiwan, about 200 m depth, Nov. 17, 1970. Sorted by Mr. Tetsuo Yoshino.

Paratype: ASM I-25362026, 20.5 mm SL, off coast of Waianae, Oahu, Hawaii, collected by an oblique net towing from 300 m depth at 21°26'N, 158° W. Collected by Mr. Clarke Kanakeoki.

Diagnosis: Characters other than those described in the diagnosis of the genus are as follows: vertebral count 29 + 24 (or 25 in the paratype) = 53 (or 54); scales on the lateral line and those above and below 92, 4/13 (can not be counted in the paratype because of its small size), cycloid. The dorsal rays 36 (or 37), being the smallest count among the family; all rays are almost uniform in length excepting the first short ray; the posterior 18 rays are branched; basal length is about half of SL. There are 16 anal rays, all segmented (can not be clarified), the third is the longest. The posterior 10 rays are uniform in length, with the posterior 8 rays branched. Pectoral rays are 16 (17), the upper three and the lowermost rays are simple. The pelvic rays number 5, all are segmented and the inner four rays are branched (can not be determined in the paratype), its length are 7.6 to 7.8% SL (in other genera of the family less than 4% SL); length of the pelvic girdle is 4.0% SL. The principal caudal rays number 8 + 7, out of which 7 + 6 are branched. Procurrent rays number 15 (upper) and 16 (lower). Gill rakers number 8 + 20 (not determined in the paratype). Infraorbitals number 7 (including lachrymal). Olfactory lamellae number 10 (not determined). Teeth are absent from both jaws and the roof of mouth.

Description: Body subcylindrical, with posterior portion more compressed. Body without ventrolateral skin fold. Head conical. Lower jaw protruded and upper jaw protrusile. The dorsal fin originates above the fifth vertebra and ends at the eighth caudal (= 37th) vertebra, whereas that of all other known ammodytids originates above the fourth. Two incomplete interneurals are present above the second and third neural spines. The first anal pterygiophore is attached to the rib of the last abdominal (= 29th) vertebra and the last attached to the 11th caudal (= 40th) vertebra. The last dorsal ray is branched from its base but that of the anal is distally branched two thirds of the length. The dorsal fin ends in advance of the anal fin. There are 16 caudal vertebrae posterior to the dorsal fin support, the highest count among the family. All other species have less than 13 post dorsal vertebrae. Length of dorsal fin base is 50% (53) SL, smallest among the family. The two nostrils are separated, the anterior is round and situated at the middle on the snout and the posterior is elliptical and situated just in front of the eye. The nasal cavity is large, occupying about half the snout length. Left and right cavities are separated by a thin longitudinal septum. The

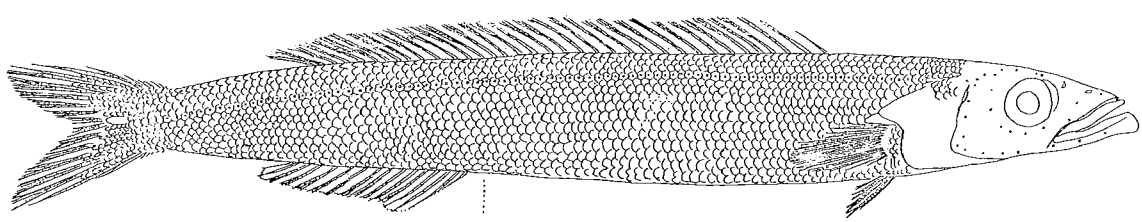

Fig. 1. Holotype of *Protammodytes brachistos* sp. nov. FSKU 701117. 86.0 mm SL, east off Taiwan ca 200 m, the stomach content of an *Etelis* sp.

lateralis system on the head is continuous and connected with the lateral line posteriorly. The occipital canal has only two openings. The sensory opening at the end of each infraorbital is not doubled. The procurrent caudal rays are supported by the last three neural spines, the two epurals, the stegural above and by the last four haemal spines below. Principal caudal rays are 8+7 in number and are supported by the five hypurals and the parhypural. Caudal concavity is 7.8% SL, 3.2 in HL. The urostyle and the third and fourth hypurals are fused into a single bone. Color of the preserved specimen is uniform straw yellow and lacking any body or fin markings in the holotype but in the paratype, tiny melanophores are scattered on the whole body and on the caudal fin. The pelvic fin is 7.6 to 7.8% of SL, and the distance from the snout tip to the dorsal origin is 30.3 to 31.2% (Table 1), these values are the largest ones among the known ammodytids.

Remarks: The new species is clearly distinguishable from its Atlantic counterpart by its robust body, fewer dorsal fin rays (36 or 37 vs 43 or 45), longer predorsal length (ca 30 vs 25% SL) in outer morphology, fewer abdominal vertebrae (29 vs 33), and numerous postdorsal vertebrae (16 vs 13) in internal morphology.

Status of the new genus

Characters such as a less vestigial pelvic fin, more than 7.6% SL, squamation not arranged to form diagonal straight lines, less specialized olfactory organ, absence of oblique dermal plicae, branched rays of dorsal and anal fins found in *P. brachistos* and the former *E. sarisa* contrast with the other species of the family and require recognition of a new taxon. Adding to these characters, the present new genus also has a complete series of infraorbitals, a less elongated body, neural and haemal spines of caudal vertebrae which are not expanded, two predorsals, an absence of labial ossicles, and less specialized dentary and scales. Thus, the new genus may be regarded as the most primitive or generalized one among the family Ammodytidae.

Lepidammodytes gen. nov.

Type species: *Lepidammodytes macrophthalmus* new species.

Diagnosis: Distinguishable from all other genera by the presence of a perforation on the lacrimal, ctenoid scales, and of pelvic fins. Scales on the lateral line with a tube and deeply indented centrally on posterior margin, numbering 109 to 117. Neural and haemal spines of the caudal vertebrae are not expanded. Infraorbitals complete and bold. Perforation of the dentary large, both the depth and length of the perforation exceed more than half of the entire depth and the length of the bone. The dentary ends in a pointed anterior projection. The operculo-mandible canal of the lateralis system ends in a small conical bone elevation situated just behind the anterior dentary projection. Ventro-lateral skin fold and plicae absent. Labial tissues not ossified, but bold and fit the space surrounded by blade-like projection and perforation of the dentary. Olfactory lamellae slightly reduced, occupying almost all at posterior one-third of the nasal cavity.

Remarks: The lachrymal perforation is round and receives lateral nodule of the lateral ethmoid. No other genera of the family has such perforation.

Lepidammodytes macrophthalmus sp. nov.

(Figs. 2, 3E, 4C, 5D, 7D, 9D, 10D, 11C, 12C, 13D, 14C; Table 1)

Holotype: BPBM 24261 a, 147 mm SL, Hawaiian Island trawled.
Paratypes: BPBM 24261 b, 136 mm SL, collected with the holotype. BPBM 26549, 159 mm SL, Leeward Hawaiian Islands, Maro Reef, 200 m, 22 Jan. 1981, trawled (this specimen was cleared and stained with alizarin red S). BPBM 24861 a, 144 mm SL, Hawaiian Islands, trawled, BPBM 24861 b, 149 mm SL.

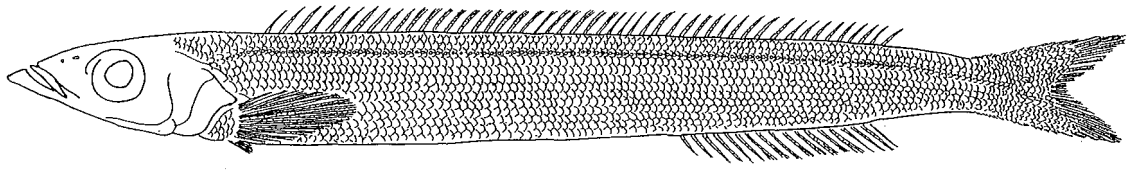

Fig. 2. Holotype of *Lepidammodytes macrophthalmus* sp. nov. BPBM 24261a. 147 mm SL, Hawaiian Island, ca 200 m, trawled.

Table 1. Counts and measurements (in hundredths of standard length) of *Protammodytes brachistos* sp. nov. and *Lepidammodytes macrophthalmus* sp. nov.

Character	*Protammodytes brachistos*		*Lepidammodytes macrophthalmus*				
	holotype	paratype	holotype	paratypes			
	FSKU 701117	ASEM-I 2536026	BPBM 24261a	BPBM 24261b	BPBM 26549	BPBM 24861a	BPBM 24861b
D	36	37	48	50	51	48	51
A	16	17	19	18	18	19	19
P1	16	16	15	15	15	15	16
P2	5	5	5	5	5	5	5
prc C ray[1]	15/16	?	16/15	17/17	17/17	16/15	16/16
Vert.	29+24	29+25	36+26	36+26	36+26	36+26	36+27
prDV/poDV[2]	5/16	5/16	4/12	4/13	4/12	4/12	4/13
post AV[3]	13	13	13	13	12	13	13
LLS	92	?	116	116	112	117	109
Ltr	4/13	?	3/12	3/12	3/12	3/12	3/11
Gr	8+20	?	7+23	7+21	8+21	7+22	8+21
Brst	5+2	5+2	5+2	5+2	5+2	5+2	5+2
SL mm	86.0	20.5	147	136	159	144	149
HL %	24.5	25.4	21.8	23.2	20.8	22.9	22.3
UJL	8.52	8.78	6.32	6.76	6.10	6.39	6.37
ED	4.43	4.77	5.00	6.03	4.96	5.62	5.83
SntL	7.34	7.79	6.46	6.69	6.16	6.18	6.17
BD D.org	12.9	13.6	10.2	10.9	9.86	10.6	10.5
A.org	11.9	12.7	10.5	10.4	10.2	10.9	10.5
OPD	6.2	7.8	5.50	5.44	5.03	5.55	5.10
CPL	10.5	10.7	13.3	13.4	12.1	13.1	12.6
P1L	10.0	11.7	12.2	13.2	12.1	11.2	12.1
P2L	7.62	7.78	4.01	3.01	3.65	3.42	3.01
Snt-D	30.3	31.2	23.8	23.6	22.1	23.2	23.9
Snt-A	61.6	61.5	69.4	71.3	67.9	68.4	68.4
D base	50.2	53.6	60.5	63.9	64.1	61.5	61.1
A base	18.0	20.0	17.6	18.4	18.8	17.4	17.2
C concavity	7.81	?	6.65	6.89	6.41	6.94	6.58

[1]procurrent caudal rays: upper/lower.
[2]vertebrae anterior to dorsal fin/those posterior to dorsal.
[3]vertebrae posterior to anal fin.

Diagnosis: Characters other than those described in the diagnosis of the genus are as follows: A species of the family Ammodytidae with a moderately elongate body having 36 abdominal and 26 or 27 caudal vertebrae, totaling 62 or 63 vertebrae (the family ranges from 52 to 72); 48-51 dorsal rays; 23-24 anal rays; small elvic fin, 3-4% SL, 5 rays, all segmented; lateral line scales 109-117; transverse scale rows 4/12 or 13, smallest count within the family, no scales on upper edge of the opercle; gill rakers 7-8 + 21-23; eye large, 5 to 6% SL, one quarter of head length; lachrymal large 5.3 to 5.6% SL, one quarter of head length. Color in alcohol uniformly straw yellow, no body or fin markings.

Description: The dorsal fin originates above the 5th vertebra and ends at the 15th caudal (= 51st) vertebra. Two incomplete interneurals are present on the second and third neural spines. The first anal pterygiophore is attached to the rib of the last abdominal (= 36th) vertebra and the last attached to the 16th caudal (= 52nd) vertebra. Both the last dorsal and anal rays are branched at their base. The dorsal fin ends slightly in advance of the anal fin. There are 12 or 13 vertebrae posterior to the dorsal fin support. Dorsal rays 48 (48-51), rays of 11th to 27th (9-28) branched, other rays simple, first ray short, other rays similar in length; anal rays 19 (18-19), several rays of central part branched, anterior two rays short; pectoral rays 15, upper and lower two rays simple, pelvic rays 5; principal caudal rays 8 + 7, of which 7 + 6 are branched; caudal procurrent rays 16/15 (16/15 to 17/17), posterior three segmented, caudal con-

cavity 6.5 to 6.9% SL, about one third of the head; lateral-line scale 116 (109-117); scales above lateral line 2 1/2 at dorsal origin; scales below lateral line 12 (12-13) at anal fin origin; gill rakers 7 + 23 (7-8 + 21-22); branchiostegals 7; vertebrae 36 + 26 (36 + 26-27); predorsal vertebrae 4; postdorsal vertebrae 12 (12-13); post anal vertebrae 13 (12-13); neural and haemal spines of caudal vertebrae not expanded; predorsals 2, on 2nd and 3rd vertebrae; first two dorsal pterygiophores in space between 4th and 5th neural spines; lateralis system on head continuous excluing a small gap below the middle of the eye.

Body moderately elongate, body depth 10.2% SL (9.86-10.9) at dorsal origin and 10.5% (10.2-10.9) at anal origin, trunk subcylindrical and slightly compressed posteriorly; without longitudinal ventro-lateral skin fold; head pointed, length 21.8 % SL (20.8-23.2).

Bleekeria

Diagnosis: Distinguishable from other genera of the family Ammodytidae by the presence of teeth on jaws and by fewer dorsal (39-43) and anal (13-18) rays. The ventro-lateral skin fold is slightly developed. The subocular sensory canal is complete and the lateralis system on the head is continuous with that on the body. Labial tissues are not ossified. The predorsal bone is absent. Haemal and neural spines of caudal vertebrae are not expanded. Olfactory rosette consists of five reduced lamellae.

Remarks: The genus *Bleekeria* consists of three species, viz. *B. mitsukurii, B. kallolepis*, and *B. viridianguilla*. Their distribution is restricted to tropical and temperate regions of the Indo-west Pacific (Day 1889, Marshall 1965).

Validity of the genus *Embolichthys* Jordan, 1903

Jordan (1903) proposed the genus based on *Bleekeria mitsukurii* Jordan et Evermann, 1902, due to pelvic fin presence. Most authors, with the exception of Robins and Bohlke (1970), follow Jordan (1903). Robins and Bohlke doubted the validity of the genus *Embolichthys*, stating "*Bleekeria* and *Embolichthys* are similar in all features except presence or absence of pelvic fins and may merit no more than subgeneric ranking." We agree with them because we failed to find any conspicuous difference between *Bleekeria* and *Emobolichthys*, except for the pelvic fin; *B. mitsukurii* and *B. viridianguilla* show the closest similarities in characters including osteological features and meristic counts, dentition, and squamation among the species here treated.

B. mitsukurii is widely distributed in the western Pacific, from the Malacca strait to the Pacific coast of Central Japan. *B. viridianguilla* is also distributed widely from the waters around Taiwan to the Gulf of Thailand westward, and to the coast of Queensland southward. On the contrary, *B. kallolepis* is reported from only the southern coast of India (Madras). Our specimen from the southern Andaman Sea extends the distribution range of the species. Gunther (1862) reported toothless jaws of *B. kallolepis*, but our specimen from the Andaman Sea has bands of fine canines on both jaws. Fowler (1953) described *B. viridianguilla* as having minute teeth on jaws. Though the teeth of *Bleekeria* are very fine and younger specimens are lack dentigerous jaws, we found teeth in all three species of the genus *Bleekeria*.

Species key for the genus *Bleekeria* is presented below

1a. Margin of upper and lower caudal fin black; 3 scale rows above the lateral line at dorsal origin lateral line; those below the lateral line at the anal fin origin 15 or 16; less than 100 lateral line scales; distributed from Madras to the west coast of Malay penninsula ..... *Bleekeria kallolepis*

1b. Margin of upper and lower caudal fin lobes without black margin; 4 scale rows above the dorsal origin lateral line, those below lateral line at anal origin 21 to 23; lateral line scale about 100 (108-117); western Pacific distribution 2

2a. Pelvic fin present; Singapore to central Japan distribution ..... *B. mitsukurii*

2b. Pelvic fin absent; Queensland to Taiwan distribution ..... *B. viridianguilla*

Ammodytoides

Diagnosis: Distinguishable from other genera of the family by the number of fin rays, i.e., 45-50 dorsal and 21-25 anal rays. Ventro-lateral skin fold is slightly developed. The subocular canal is discontinuous below the eye. The lateralis system on head is discontinuous with the lateral line in the posttemporal region. Labial ossicles and predorsal bones are present. Haemal and neural spines of caudal vertebrae are expanded. Olfactory rosette is absent.

The status of genus *Ammodytoides* Duncker and Mohr, 1939

In their revision of the family Ammodytidae, Duncker and Mohr (1939) stated "V fehlend. a. Merkmale von *Ammodytes*, jedoch ohne ventrolaterale Hautsaume (*Bleekeria* McCulloch and Waite 1916, nec Gunther 1862). 5. *Ammodytoides* g. n.?

b. Zwei ——" Their description was very short but the first proposal of the genus *Ammodytoides*, recognizing *Bleekeria vagus* as a species. Characters such as the presence of labial ossicles, absence of olfactory lamella, presence of the pelvic girdle, and the elongation of the body accompanied with an increment in the number of vertebrae and dorsal and anal fin rays necessitates the discrimination of the group from the former *Bleekeria*. The genus *Ammodytoides* includes *A. gilli, A. kimurai, A. lucasanus, A. pylei, A. renniei*, and *A. vagus* while *Bleekeria* includes *B. kallolepis, B. mitsukurii*, and *B. viridianguilla*. As far as the authors are aware the name *Ammodytoides* could not be found in the literature with the exception of their original description and two very recent papers by the junior author (Randall et al. 1993, Ida and Randall 1994), still the specialized characters above mentioned seem to be enough for the recognition of a separate taxon.

Gymnammodytes

Diagnosis: Distinguishable from other genera of the family, by the absence of scales on most of the body. A ventro lateral skin fold is developed. The subocular sensory canal is widely discontinuous below the eye. The lateralis system on the head is not continuous with the lateral line in the posttemporal region. The lateral line is branched both dorsally and ventrally. The caudal peduncle is the shortest in the family. Labial ossicles are present. Predorsal bone is absent. Haemal and neural spines of the caudal vertebrae are expanded. Olfactory rosette is absent.

Remarks: The genus *Gymnammodytes* consists of three species, viz. *G. capensis, G. cicerelus*, and *G. semisquamatus*. These three species are confined to the eastern Atlantic and Mediterranean and its adjacent waters. Regarding latitudinal distribution, they range from 60°N to 40°S, showing the widest distribution in latitude among members of the family.

Ammodytes

Diagnosis: Distinguishable from other genera of the family by the combination of the following characters: fine scales (125-165 on lateral line) embedded deeply in dermal plicae, labial tissues not ossified, predorsal bones absent, tip of the prevomer straight, not protruding from the roof of the mouth. Subocular canal is interrupted widely below the eye. The lateral line is not continuous with that on the head. Predorsal bones are absent. Neural and haemal spines of caudal vertebrae are not expanded.

Remarks: The genus *Ammodytes* shows the widest distribution among the family, from temperate to boreal waters. But none of the species is found in the southern hemisphere. Synonymy of the species of the genus is yet to be clarified.

Many authors have reported on the extraordinary variation of meristic features among the species of the genus *Ammodytes* (e.g., Richard et al. 1963, Hatanaka and Okamoto 1950). Adding to this variability, there exists a smaller difference in osteological characters within the genus (Figs. 7, 10); the identification of the species of *Ammodytes* should be based on characters other than osteological or meristic ones. Morphometry, electrophoretic analysis of isozymes, and molecular analysis seem to be needed. Reay (1986) clearly shows the difference in squamation on the belly and caudal base between *A. tobianus* and *A. marinus*. Recently, Nizinski et al. (1990) have separated two sympatric species of *Ammodytes* from the northwest Atlantic by a combination of numbers of plicae and vertebrae (Nizinski et al. 1990).

Conventionally, most authors apply the name *A. hexapterus* to the eastern and northern North Pacific specimens having higher meristic counts (Bailey et al. 1970, Hart 1973) and *A. personatus* for the western North Pacific specimens having lower meristic counts (Matsubara 1955, Masuda et al. 1984). *A. personatus* was originally described for specimens from the west coast of North America (Girald 1859). Most authors have synonymized *A. personatus* with *A. hexapterus* but McAllister (1960) recognized the specific distinction of *A. personatus* from *A. hexapterus*. More than a half dozen of nominal species have been established for the Pacific *Ammodytes* (Richards et al. 1963). Although for the above mentioned reason, the name of *A. personatus* can not be used for the Japanese species, we tentatively use *A. personatus* for Japanese species because research for a suitable name for the Japanese *Ammodytes* is still in progress.

Hyperoplus

Diagnosis: The genus is distinguishable from other genera of the family by the nonprotrusible upper jaw and curved prevomer protruded from roof of the mouth. Scales are very fine, about 170 on lateral line, deeply embedded in dermal plicae. Labial tissues are not ossified. Predorsal

bones are absent. The subocular canal is interrupted widely below the eye. The lateralis system on the head is discontinuous with that on the body in the posttemporal region. Neural and haemal spines of caudal vertebrae are expanded. Excepting the nonprotrusible upper jaw and protruded prevomer, the genus shows closest affinity to genus *Ammodytes*.

Remarks: The genus *Hyperoplus* consists of two species, viz. *H. lanceolatus* and *H. immaculatus*. Both species appear in the northeastern Atlantic, but distribution of the latter species is restricted to the waters around England. Reaching 40 cm SL, it is the largest within the family.

DESCRIPTION OF THE CHARACTERS

Lateralis system (Fig. 3): Fishes of the genera *Protammodytes* and *Bleekeria* have a complete subocular canal and no discontinuity could be found (Figs. 3A, B). Supraocular canals on both sides meet at a point above the posterior part of the eye. Branches of the canal and their operculomandibular and supratemporal openings are simple and large in *P. brachistos* and *P. sarisa* but slightly complicated and fine in *B. mitsukurii* and *B. viridianguilla* (Figs. 3B, C).

Fishes of the genus *Ammodytoides* have a narrow disjunction in the subocular canal just below the eye (Figs. 3F, G). Three patches of pit organs are present on the disjunctional part in *A. pylei* (Fig. 3F).

Fishes of the genera *Gymnammodytes, Ammodytes*, and *Hyperoplus* have two disjunctions in the lateralis system in the subocular region and above the shoulder region. The subocular disjunction is wide and bears several patches of pit organs excluding *G. capensis* in which the organs were not recognized due to the poor condition of the specimen. Another disjunction behind the posttemporal has no apparent sense organ (Figs. 3H-L).

Lateral line (Fig. 4): Most species have a simple tubular lateral line (Figs. 4A-D), but in fishes of the genus *Gymnammodytes*, the lateral line has branches both dorsally and ventrally (Fig. 4F). Fishes of the genera *Bleekeria, Ammodytoides, Ammodytes*, and *Hyperoplus* (Figs. 4D, E, G, H) have patches of additional sensory villi just above the lateral line. They are placed on every two or three scale rows and are present throughout below the base of the dorsal fin and become less regular in the posterior part.

Squamation and skin fold: Scale arangement and details of scales of the fishes of the family are illustrated in Fig. 4. The posterior edges of scales, with the exception of the species of genera *Protammodytes* and *Gymnammodytes*, are arranged to form diagonal straight lines. A ventro-lateral skin fold is developed in the genera *Gymnammodytes, Ammodytes*, and *Hyperoplus*.

Apparently, scales are not embedded in the dermal layer in *Lepidammodytes* or *Protammodytes* (Figs. 4A,C), but in fishes of the genera of *Bleekeria, Ammodytoides, Ammodytes*, and *Hyperoplus*, scales are embedded in more or less oblique dermal plicae. In *Bleekeria*, the plicae are thin and scales are recognized, but less so than in the fishes of genus *Ammodytoides*. In species of *Ammodytes* and *Hyperoplus*, the plicae are well developed and scales are completely embedded in the plicae and are hardly recognizable.

Protammodytes: One of the most striking features of this group, distinguishing it from other groups, is that the squamation is not arranged to form diagonal straight lines (Fig. 4A). Scales of *Protammodytes* are less vestigial and are relatively large among members of the family. Scales on the oblique rows are arranged 5-1-13 and those on the lateral line number 92 in *P. brachistos* and those are 4-1-16 (originally reported as 4-1-9, but the paratype was reexamined by us) and 95 respectively in *P. sarisa*. There is little size difference between the scales from different parts of the body in these two species. A patch of scales is present on the upper part of the preopercle.

Bleekeria: The posterior edges of the scales are arranged in straight lines. The size and shape of the scales on the body is rather variable. *Bleekeria kallolepis* has the largest largest scales in the genus. Scales on the transverse row are arranged in 3-1-14, and those on the lateral line number 100. Scales of *B. mitsukurii* are slightly larger than those of *B. viridianguilla*. The former species has 4-1-18 transverse and 109 to 119 longitudinal scales, and the latter has 5-1-22 and 108 to 118 scales. A row of scales is present on the posterior margin of the preopercle (Figs. 3B-D).

Lepidammodytes: Scales of this genus are rather small, about 114 on the lateral line and 4-1-12 (or 13) in the transverse row. Scales are absent from the opercle (Fig. 3E).

Ammodytoides: The size of the scales is smaller than those of the genus *Bleekeria*, and larger than those of *Ammodytes*. The scales are oval in their shape and there is little difference in shape and size throughout the body. Scales on the transverse row are arranged in 3-1-17, and those on the longi-

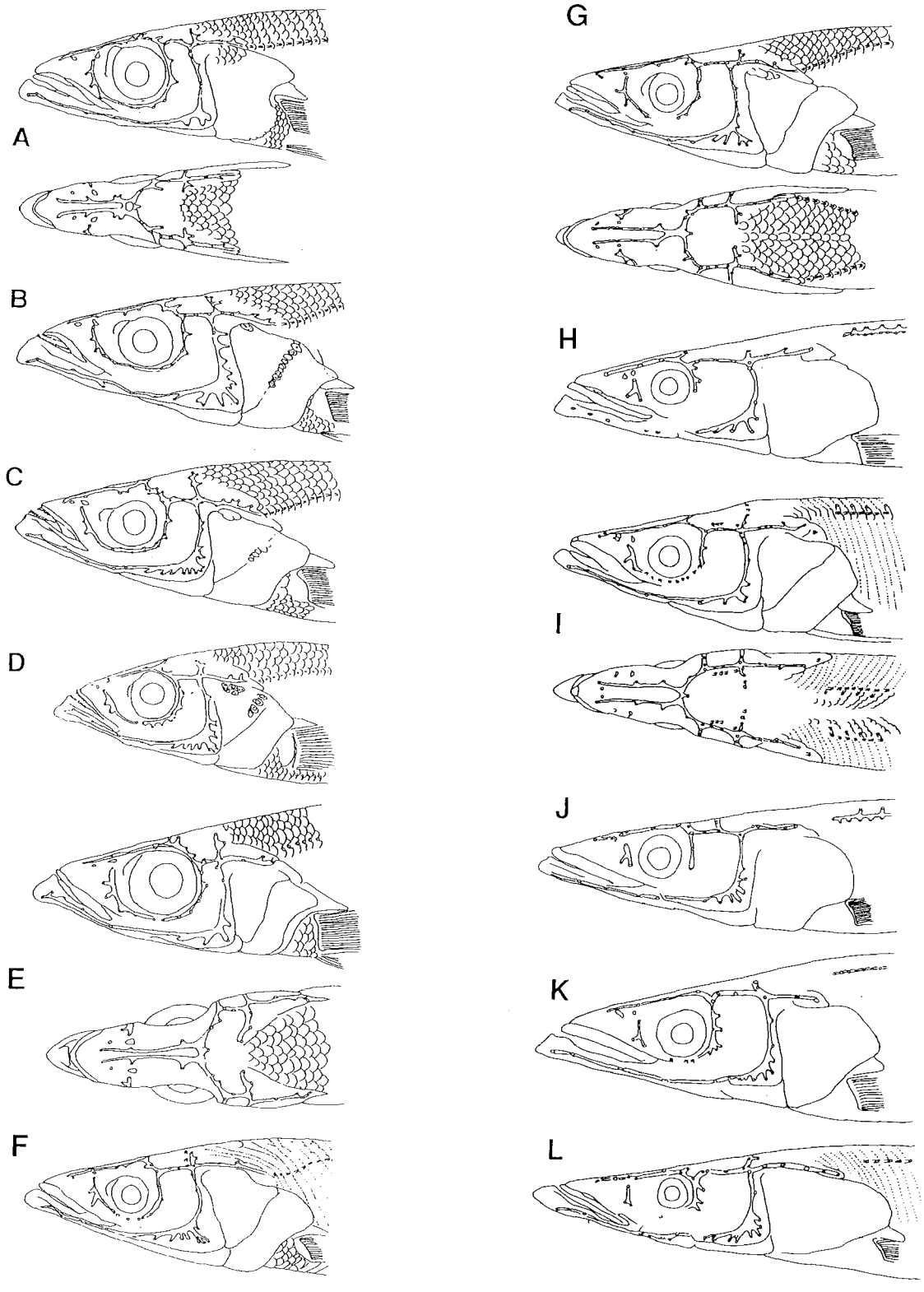

Fig. 3. Lateralis system of the head and anterior lateral line of the fishes of the family Ammodytidae. A: *Protammodytes brachistos*, B: *Bleekeria mitsukurii*, C: *B. viridianguilla*, D: *Bleekeria kallolepis*, E: *Lepidammodytes macrophthalmus*, F: *Ammodytoides lucasanus*, G: *A. vagus*, H: *Gymnammodytes capensis*, I: *G. cicerelus*, J: *Ammodytes personatus*, K: *A. tobianus*, L: *Hyperoplus lanceolatus*. Note wide disjunction in *Gymnammodytes, Ammodytes*, and *Hyperoplus*. Scales present on the preopercle in *Protammodytes* and *Bleekeria*.

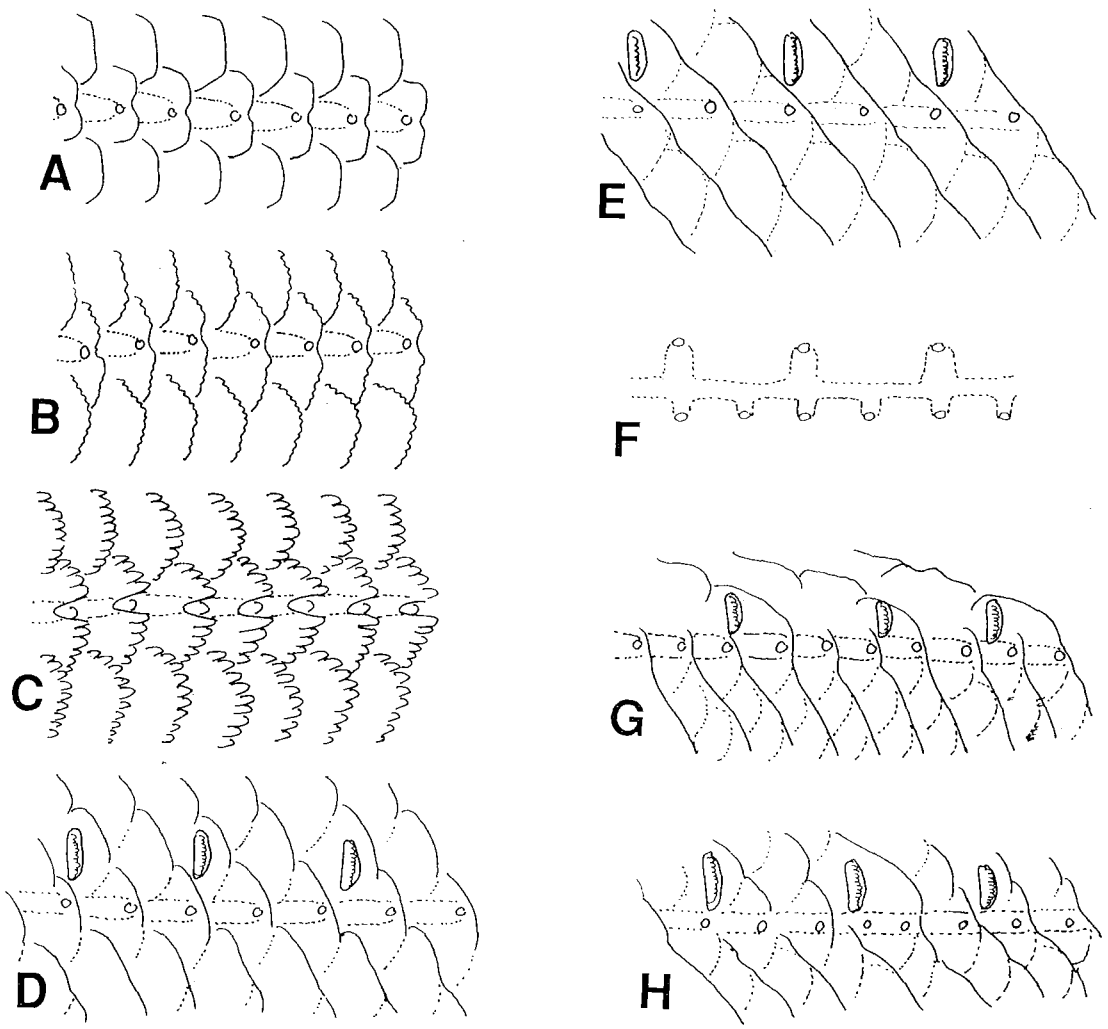

Fig. 4. Squamation and lateral line of some selected ammodytid fishes. Note the presence of well developed oblique dermal plicae in genera of *Ammodytes* and *Hyperoplus*. The plicae are less developed in genera of *Bleekeria* and *Ammodytoides*. A: *Protammodytes brachistos*, B: *Bleekeria kallolepis*, C: *Lepidammodytes macrohthalmus*, D: *Bleekeria mitsukurii*, E: *Ammodytoides vagus*, F: *Gymnammodytes semisquamatus*, G: *Ammodytes personatus*, H: *Hyperoplus lanceolatus*.

tudinal row number 118 in *A. pylei*. They are 3-1-14 and 101 to 108 in *A. lucasanus*, 3-1-18 and 112 in *A. vagus*, 2-1-15 and 113 to 120 in *A. renniei* (Smith 1957), 3-1-14 and 97 in *A. gilli* (Bean 1985). The ventro-lateral skinfold is absent from this genus. Scales are absent from the opercular region (Figs. 3F,G).

Gymnammodytes: Scales are most degenerate within the family *Ammodytidae*. Most species lack scales on the side of the body, but tubular lateral line scales are retained. The posterior 1/6 of the body lacks a lateral line. Lateral line scales number 105 to 110 in *G. semisquamatus*. Adding to the lateral line scales is a patch of small scales present on the posterior part of the body. Lateral line scales are 92 to 102 in *G. capensis* and 100 to 114 in *G. cicirelus*. There are no scales on the whole body except the lateral line in these two species. The ventrolateral skinfold is present in all species of the genus. The skinfold is less developed and extends slightly beyond the pectoral fin tip in *G. semisquamatus* and *G. capensis*, whereas in *G. cicerelus*, the fold is well developed and extends to a point above the anterior base of the anal fin.

Ammodytes: Scales of this genus are rather small, about 110 to 170 in the longitudinal series. Length of scales on the anterior body is much shorter than the height, scales below the lateral line do not overlap longitudinally, but do obliquely.

Scales on the lateral line are about 160 to 170 in *A. personatus*, 128 to 130 in *A. hexapterus*, and 120 to 129 in *A. tobianus*. Scales on transverse rows could not be counted due to their small size, about 4 above the lateral line and 40 below. The lateral line ends slightly before dorsal fin insertion. The ventro-lateral skinfold extends nearly to the point above the anal fin insertion point in *A. personatus, A. hexapterus*, and *A. tobianus*.

Hyperoplus: The lateral line extends to the caudal peduncle and about 165 to 170 scales are present on the lateral line. The ventro-lateral skinfold does not reach to the point above the middle of anal fin base.

Thin and fine scales of Ammodytidae are illustrated in Fig. 5 and are cycloid or weakly ctenoid. Circuli are dense on the anterior portion and less so on the dorsal and ventral portions. The posterior, i.e., exposed margin is rather smooth in *Protammodytes brachistos* (Fig. 5A), but it is finely indented in *P. sarisa* and all the species of genera *Bleekeria* and *Ammodytoides* (Figs. 5C-E). In these species, there are very fine perforations on the posterior part of scales. Scales of *Lepidammodytes* are unique among the family in that the posterior margin is roughly crenulated and the tubed lateral line scale is deeply notched (Fig. 5D). In species of the genera *Ammodytes* and *Hyperoplus*, scales other than those on the lateral line are much smaller than those on the line (Fig. 5E).

Fin rays: Counts of pectoral fin rays in the fishes of the Ammodytidae are shown in Table 2. Most species have 15 pectoral rays of which the upper and lower two rays are undivided. *Ammodytoides pylei* is unique in having 16 or 17 rays, the highest count within the family. Fishes of the genera *Gymnammodytes* and *Hyperoplus* have 13 or 14 rays. *Ammodytes hexapterus* and *A. personatus* have 13 to 15 rays (modally 14), but the North Sea species, *A. tobianus* and *A. marinus* have 12 to 13 rays, the lowest count in the family.

Dorsal and anal fins (Fig. 6): as can be seen in the figure, most species are grouped in related clusters with the exception of the genus *Protammodytes* in which the two species are separated by the genus *Bleekeria*. Genera having fewer rays show a wide variation in anal fin ray counts, whereas those having numerous fin rays show wide variation in the dorsal fin ray counts. Fishes of the genera *Protammodytes, Bleekeria, Lepidammdytes,* and *Ammodytoides* have branched dorsal and anal rays, whereas fishes of the genera *Gymnammodytes, Ammodytes*, and *Hyperoplus* have simple rays. In *Protammodytes brachistos* most dorsal and anal rays excluding the anterior several rays, are divided, but in *P. sarisa*, only a few posterior rays are divided. In fishes of the genus *Bleekeria*, about 10 dorsal and anal fin posterior rays are divided. But, in most cases, the younger individuals lack branched rays.

Position of the origins and insertions of dorsal fin expressed as the ordinal number of the neural spines and the modal number of dorsal and anal fin rays for each species are shown in Fig. 7. In the fishes of the genera *Protammodytes, Bleekeria*, and *Ammodytoides,* the dorsal fin originates between the 4th and 6th vertebrae. But in *Gymnammodytes* and *Ammodytes*, the dorsal fin originates between the 7th and 9th vertebrae. Dorsal fin insertion is far anterior to the caudal base. The gap expressed as the number of vertebrae separating the insertion and the caudal fin base is 17 in *Protammodytes brachistos*, 13 in *P. sarisa* and all the species of *Bleekeria*, and 12 in all the species of *Ammodytoides*. In *Gymnammodytes* and *Ammodytes*, only 5 or 4 vertebrae are present between the insertion of the dorsal and caudal fin base.

The increment in the number of dorsal fin rays is defined by the posterior extension of the dorsal fin base together with the increment of the abdominal vertebrae, especially in *Gymnammodytes* and *Ammodytes*. The increment of anal fin rays is almost the same as that of the dorsal.

The caudal peduncle becomes shorter and lower with the increment of the number of dorsal and anal fin rays.

With the exception of the genera *Ammodytes* and *Hyperoplus*, fishes of the family are well differentiated by the fin formula from one another (Fig. 6). The fin formula overlaps in these two genera.

Predorsal bone (Fig. 7): Fishes of the family Ammodytidae are divided into two groups: those having two predorsals (Figs. 7A-D) and those lacking a predorsal (Figs. 7E, F). In all species of the genera *Protammodytes, Bleekeria, Lepidammodytes* and *Ammodytoides*, the first is situated just above the neural spine of the second vertebra and the second above the third neural spine (Figs. 7A-C). In species of the genera *Gymnammodytes, Ammodytes*, and *Hyperoplus*, the predorsal is absent (Figs. 7E-G).

In the former group, there are only four to five anterior vertebrae to the dorsal pterygiophores, whereas in the latter group, there are more than 7 anterior vertebrae to the dorsal pterygiophores (Fig. 7).

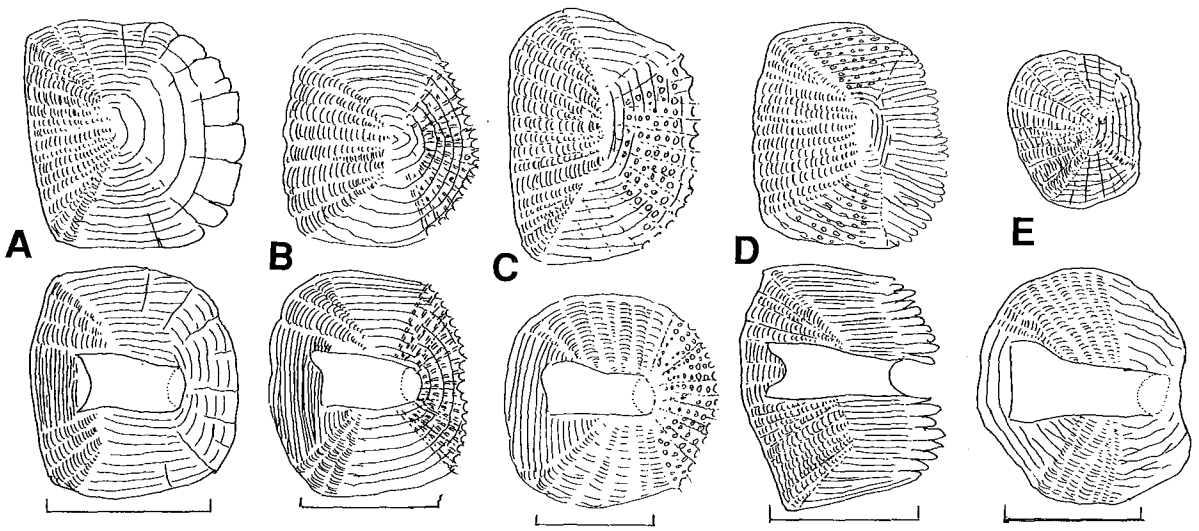

Fig. 5. Scales of some selected ammodytids. Upper figures: scales just below lateral line. Lower figures: lateral line scales below dorsal origin. A: *Protammodytes brachistos*, B: *P. sarisa*, C: *Bleekeria mitsukurii*, D: *Lepidammodytes macrophthalmus*, E; *Hyperoplus lanceolatus*. Note the size difference between scale on lateral line and that below the line in *Hyperoplus* while in other three genera, there is no such difference. Scales indicate 1 mm.

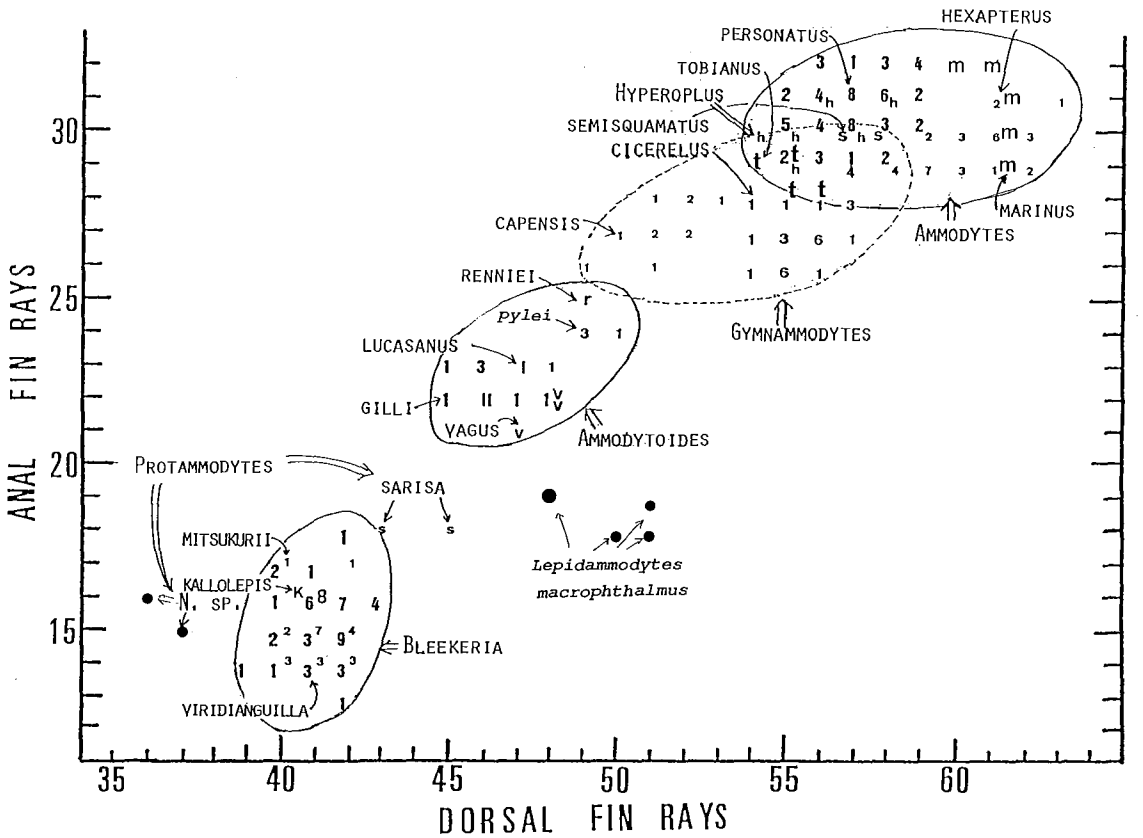

Fig. 6. Scatter diagram showing relation of dorsal and anal fin rays count among the family Ammodytidae. Note each isolated cluster of species group of *Bleekeria* and *Ammodytoides*. Species of genera of *Gymnammodytes, Ammodytes*, and *Hyperoplus* are largely overlapped.

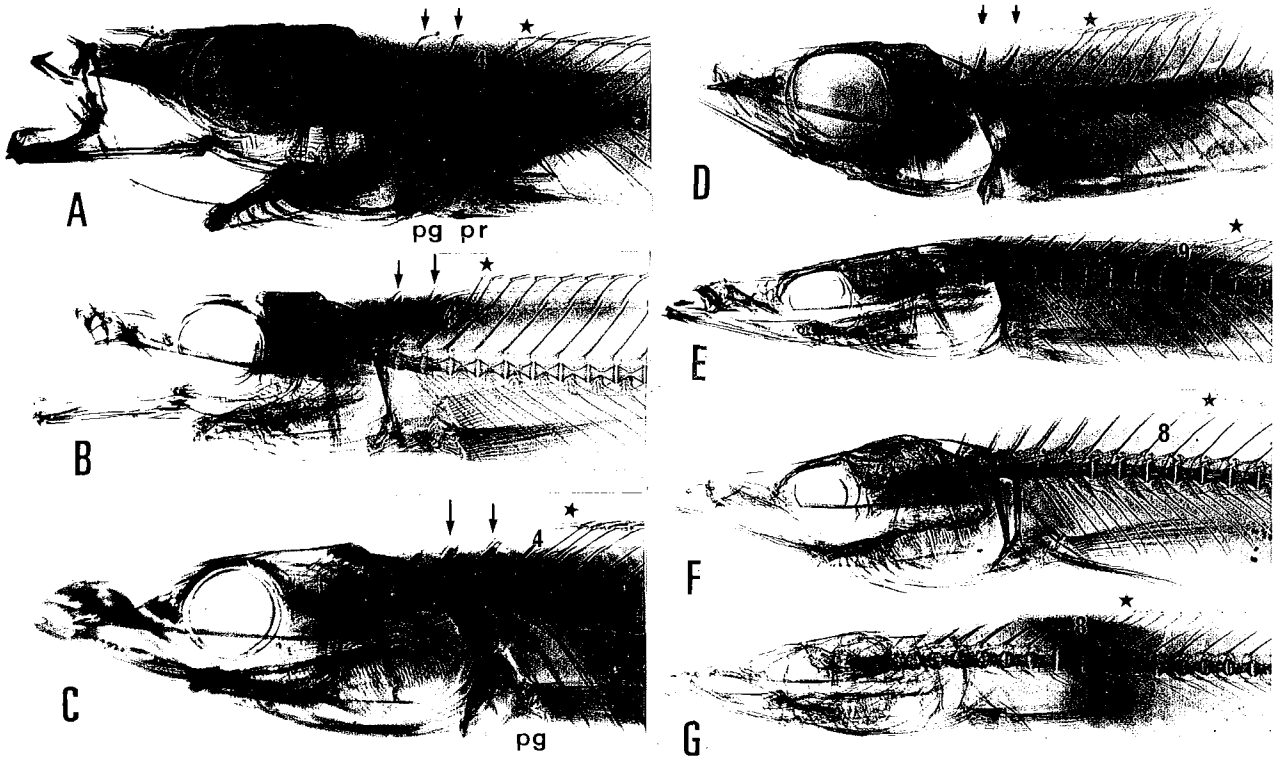

Fig. 7. X-ray photographs showing predorsal bone (indicated by arrow) and origin of dorsal fin (by star). Predorsals are present in *Protammodytes, Bleekeria, Lepidammodytes*, and *Ammodytoides* but absent in *Gymnammodytes, Ammodytes*, and *Hyperoplus*. A: *Protammodytes brachistos*, B: *Bleekeria viridianguilla*, C: *Ammodytoides vagus*, D: *Lepidammodytes macrophthalmus*, E: *Gymnammodytes semisquamatus*, F: *Ammodytes personatus*, G: *Hyperoplus lanceolatus*. Figures on neural spine show the ordinal number of vertebra. Note the presence of both pelvic gidle and fin rays in *Protammodytes* (A) and *Lepidammodytes* (D) and presence of the girdle in *Ammodytoides* (C).

Vertebral composition (Fig. 8): One of the most salient features of the ammodytids as members of the perciform fish group is the inverse relation of the number of abdominal and caudal vertebrae, i.e., the number of abdominal vertebrae is higher than that of the caudal. The range of the number of caudal vertebrae is smaller than that of abdominal vertebrae (22 to 29 vs. 27 to 47). The vertebral compositions of the 20 species of the family Ammodytidae are shown in Fig. 8. The modal count for each species is as follows:

Protammodytes brachistos	29 + (24 or 25) = 53 or 54
P. sarisa	33 + (24 or 25) = 57 or 58
Bleekeria mitsukurii	29 + 24 = 53
B. viridianguilla	29 + 24 = 53
B. kallolepis	(26 or 27) + (23 or 25) = 49 or 52
Ammodytoides gilli	33 + 23 = 56
A. lucasanus	32 + 24 = 54
A. renniei	32 + (25 or 26) = 57 or 58
A. vagus	36 + 26 = 60
A. pylei	34 + 26 = 60
A. kimurai	33 + 26 = 59
Lepidammodytes macrophthalmus	36 + (26 or 27) = 62 or 63
Gymnammodytes capensis	38 + 22 = 60
G. cicerelus	39 + 25 = 64
G. semisquamatus	42 + 25 (or 26) = 67 or 68
Ammodytes tobianus	37 + 25 = 62
A. personatus	(39 or 42) + 24 = 63 or 64
A. marinus	41 + 27 = 68
A. hexapterus	45 + 25 = 70
Hyperoplus lanceolatus	40 + 28 = 68

As can be seen in the figure, the variation of vertebral composition of the genera *Bleekeria* and *Ammodytoides* is comparatively small but that of genera *Gymnammodytes* and *Ammodytes* is larger. The *Hyperoplus* variation range is about the same as in *Ammodytes*.

It may be noted here that the vertebral variation ranges of *Bleekeria* and *Ammodytoides* are overlap slightly and those for genera *Gymnammodytes* and *Ammodytes* are overlap to a great degree; these clusters of genera are distinctly separated.

The difference in the total number of vertebrae reached 22 (50 to 72) and those of abdominal vertebrae exceeded 13 (27 to 40) whereas caudal

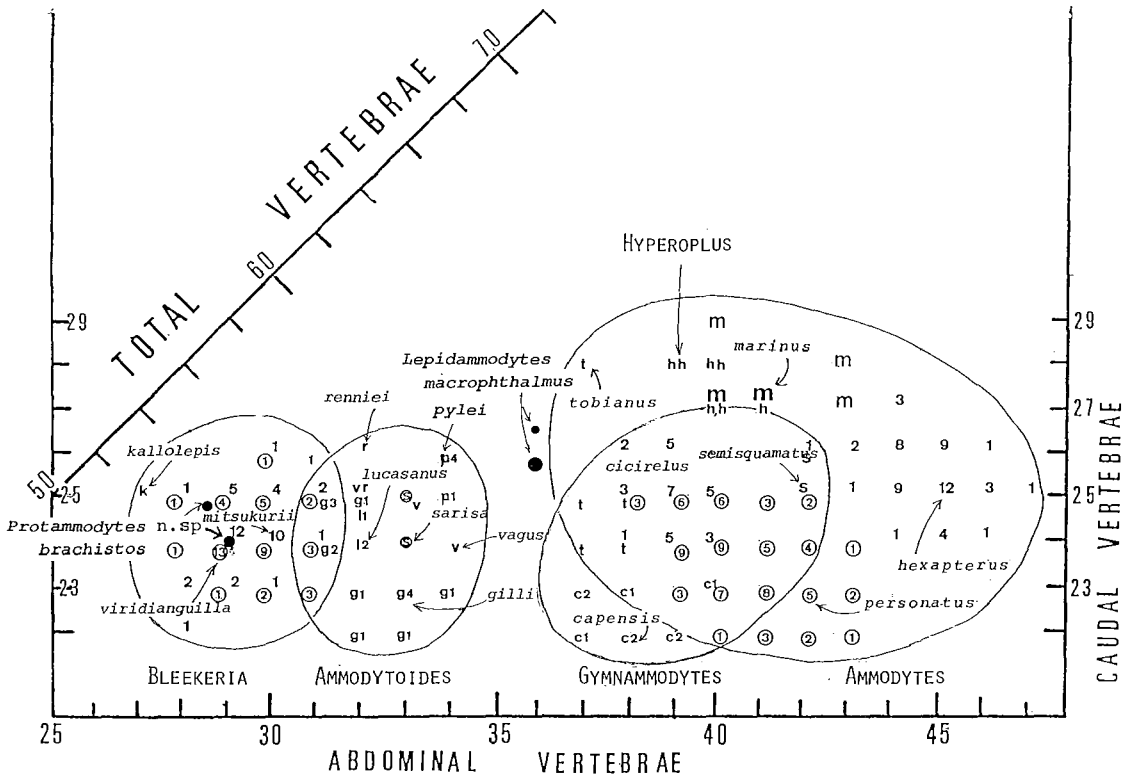

Fig. 8. Scatter diagram showing vertebral composition of fishes of the family Ammodytidae. Note tight distribution of generic groups, viz. *Protammodytes-Bleekeria-Ammodytoides* and *Gymnammodytes-Ammodytes-Hyperoplus* groups. *Lepidammodytes* intervenes the two generic groups.

Table 2. Counts of pectoral fin rays of fishes in the family Ammodytidae

Species	Pectoral fin rays				
	13	14	15	16	17
Protammodytes brachistos			1	(1)	
P. sarisa			2		
Bleekeria mitsukurii			7		
B. viridianguilla			5		
B. kallolepis			1		
Ammodytoides pylei			1	7	1
A. gilli			3		
A. lucasanus			3		
A. renniei			1		
A. vagus			1		
A. kimurai		1	5		
Lepidammodytes macrophthalmus			5		
Gymnammodytes capensis		3			
G. cicerelus		6	7		
G. semisquamatus		2			
Ammodytes personatus		1	18	4	
A. hexapterus		4	15	6	
A. marinus	2	2	2		
A. tobianus	3	2			
Hyperoplus lanceolatus		3	2		

vertebrae attained number of 7 (22 to 29). Thus the elongation of the body has occurred mainly with the increment of the abdominal vertebrae in the family Ammodytidae.

Most genera of the family, excluding *Protammodytes* and *Gymnammodytes*, are distinguishable by the number of abdominal vertebrae, but not caudal.

Shoulder and pelvic girdles: the shoulder and pelvic girdles of 10 species of the family Ammodytidae are shown in Fig. 9. The shape and elements of the girdles are typically perciform, i.e., well developed cleithrum, two postcleithra and pelvic girdle attached to the cleithrum. But, as can be seen in the figure, the pelvic fin and its girdle show gradual degeneration. The pelvic girdle and fins are less vestigial in *Protammodytes brachistos* and *Lepidammodytes macrophthalmus* (Figs. 9A, D) but the girdle becomes splint-like and the fin short in *Bleekeria mitsukurii* (Fig. 9B). Pelvic rays are absent in *Ammodytoides pylei* (Fig. 9E), condition that is quite adequate for other species of the genus *Ammodytoides*, with the exception of *A. renniei* (the presence of the girdle could not

be determined with X-ray photography due to its small size).

Pelvic rays, together with its girdle, are completely lost in *Bleekeria viridianguilla* (Fig. 9C) and in all the species of *Gymnammodytes* (Figs. 9F, G), *Ammodytes* (Figs. 9H, I), and *Hyperoplus* (Fig. 9J).

Adding to the degeneration of the pelvic fin and its girdle, a specialization can be seen in the articulation of the scapula and coracoid to the cleithrum. The articulation of these elements becomes firm in the above mentioned order; especially in fishes of genera *Ammodytes* and *Hyperoplus* in which the bones are fused into a thick plate (Figs. 9I, J).

Facial bones: The facial bones of the family show some peculiar features, such as the jaw structure and the degeneration of the infraorbitals (Fig. 10). Adding to the presence of peculiar ossicles in the oral region (Ida 1973), the articulation of the pedicel, which is equivalent to the ascending process in usual perciforms, with the premaxillary proper is unique in the family.

i) Dentition. Villiform tooth bands are present on both jaws in *Bleekeria viridianguilla, B. mitsukurii* (Figs. 10B, C), and *B. kallolepis*. In *B. mitsukurii*, the lower jaw dentition is less developed, and in

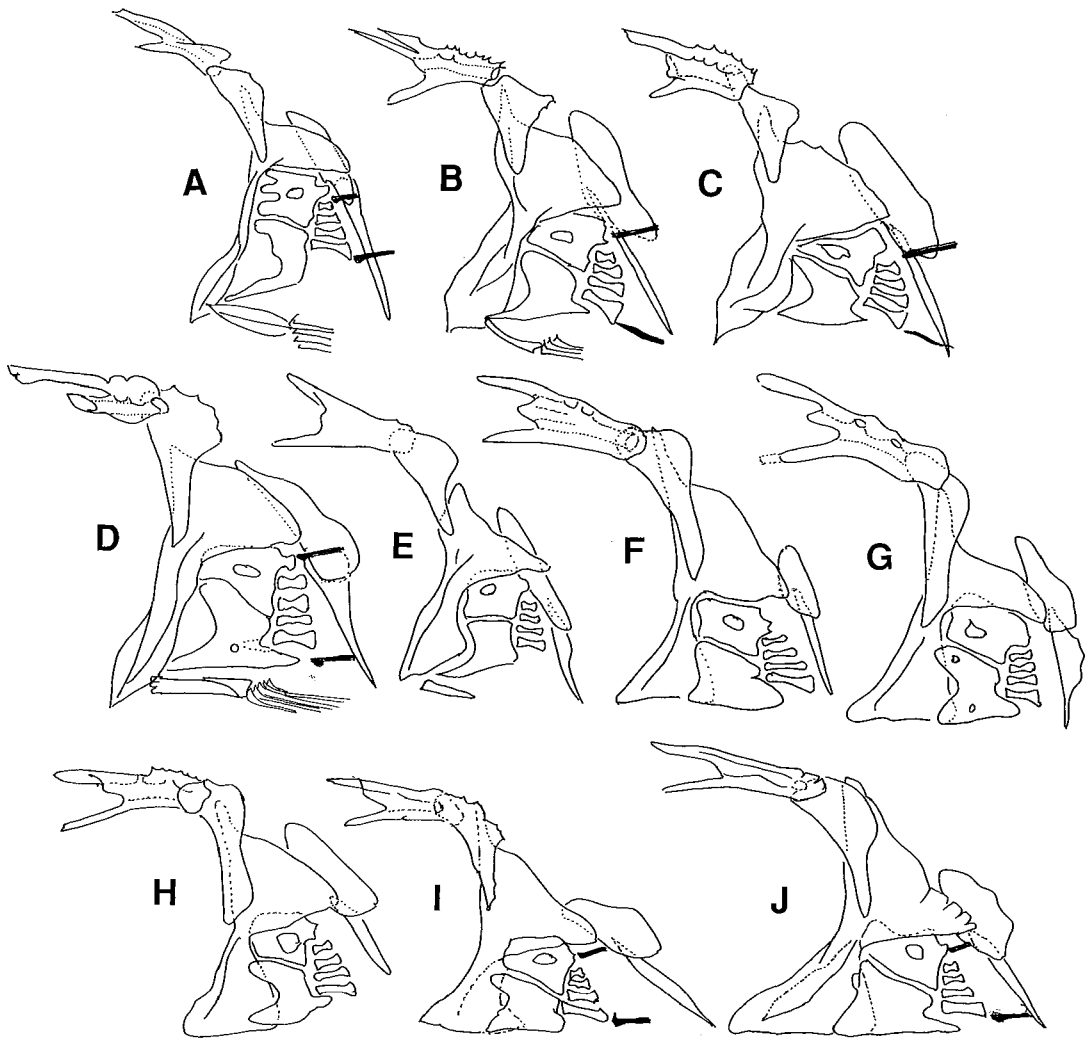

Fig. 9. Pectoral and pelvic girdles of ammodytid fishes. Both pelvic girdle and rays are present in *Protammodytes* and *Lepidammodytes*, rays are absent in *Ammodytoides* but both elements are absent in *Gymnammodytes* and *Ammodytes*. Note the posterior expansion of cleithrum against with the degeneration of the pelvic girdle in *Gymnammodytes, Ammodytes*, and *Hyperoplus* and in these genera, the lower margin of the coracoid is paralleling to the ventral contour of body. A: *Protammodytes brachistos*, B: *Bleekeria mitsukurii*, C: *B. viridianguilla*, D: *Lepidammodytes macrophthalmus*, E: *Ammodytoides pylei*, F: *Gymnammodytes capensis*, G: *G. cicerelus*, H: *Ammodytes personatus*, I: *A. hexapterus*, J: *Hyperoplus lanceolatus*.

some specimens, teeth are absent from the dentary. Excluding these three species of the genus *Bleekeria*, the family lacks teeth.

ii) Labial ossicles. Ossicles originating from cartilage in the ligaments of labial, maxillo-dentary, maxillo-vomerine, maxillo-premaxillary, and premaxillo-rostral are present in *Ammodytoides* (Figs. 10E-F); these ossicles are less developed in *Gymnammodytes* (Fig. 10G). In the genus *Ammodytoides*, six labial ossicles are present. Only one ossicle is found in the genus *Gymnammodytes* (Fig. 10F). The genera *Protammodytes, Bleekeria, Ammodytes*, and *Hyperoplus* lack these ossicles but have cartilaginous elements.

iii) Lateralis system. *Protammodytes brachistos* has seven infraorbitals (Fig. 10A, including lachrimal). They are stiff and bold, and the third one has a midpoint opening. The opening and the interspaces between the infraorbitals correspond to the apertures of the lateralis system

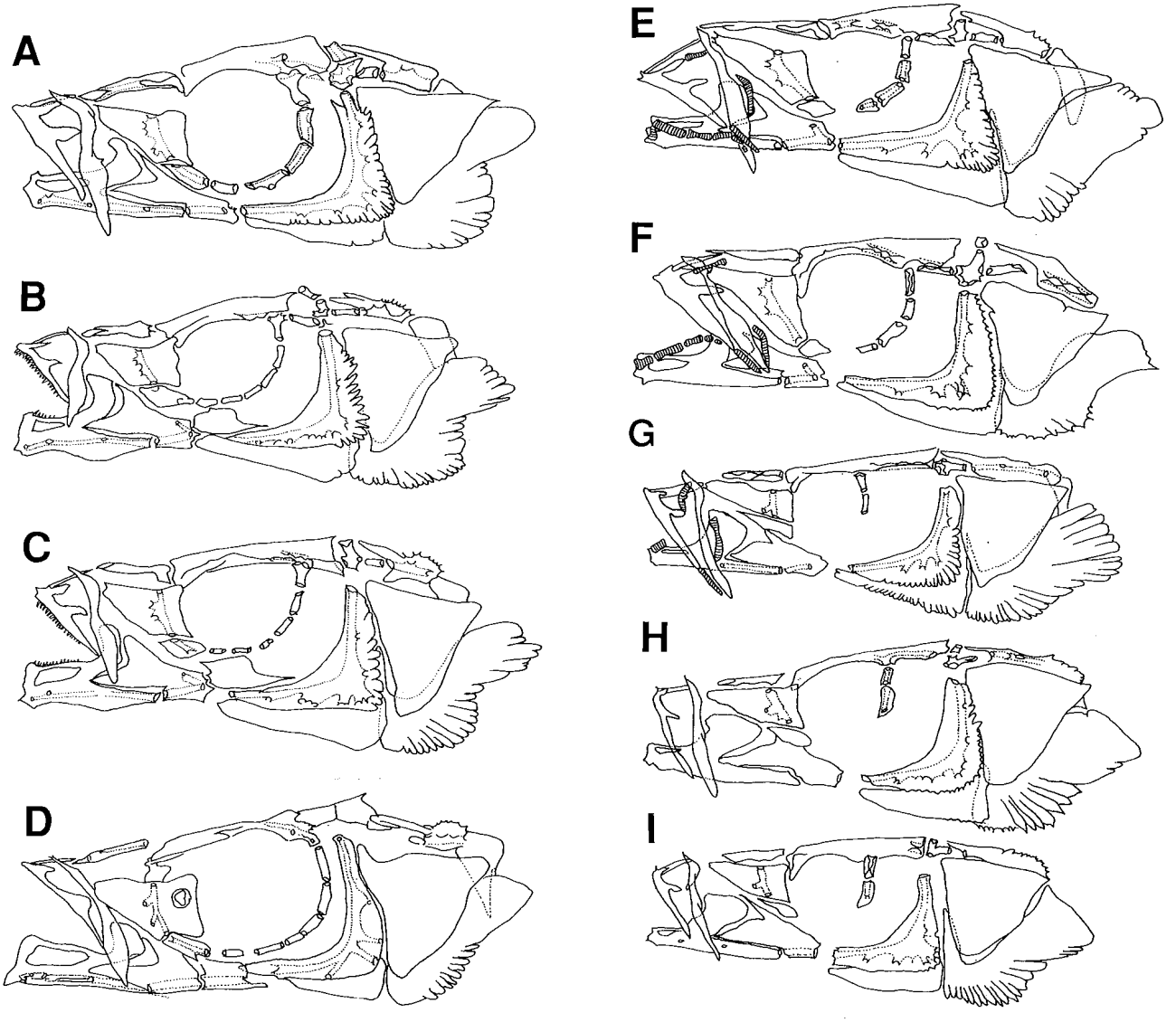

Fig. 10. Facial bones of ammodytid fishes. Teeth are present in species of *Bleekeria* (B, C) but are absent in all other species of the family. Labial ossicles are present in *Ammodytoides* (E, F) and *Gymnammodytes* (G) reducing in number in the latter genus but absent in other five genera. Note tendency of reduction of infraorbitals: in genera of *Protammodytes, Bleekeria*, and *Lepidammodytes* (A-D) eye ball is completely encircled by the continuous series of infraorbitals, but the series is broken more or less in *Ammodytoides* (F, D), *Gymnammodytes* (G), and *Ammodytes* (H, I). A: *Protammodytes brachistos*, B: *Bleekeria mitsukurii*, C: *B. viridianguilla*, D: *Lepidammodytes macrophthalmus*, E: *Ammodytoides pylei*, F: *A. vagus*, G: *Gymnammodytes capensis*, H: *Ammodytes personatus*, I: *A. hexapterus*.

(Fig. 3A). In *Bleekeria mitsukurii* and *B. viridianguilla*, infraorbitals number eight and their structure is a thin tube excluding the lachrimal, the first is plate-like (Figs. 10B, C). Those of *Lepidammodytes macrophthalmus* are same in number with *Bleekeria* but more thick and bold. Those of the species of genus *Ammodytoides* are relatively larger within the family, but number six, less by one than in the genus *Protammodytes*. The position occupied by infraorbital 2 is vacant in genus *Ammodytoides* (Figs. 10E, F). They are reduced into four in genera *Gymnammodytes* (Fig. 10G), *Ammodytes* (Figs. 10H, I), and *Hyperoplus*.

iv) Jaw structure (Fig. 11). One of the peculiar features of the family is that the ascending pedicel of the premaxillary is heterogeneous compared with the premaxillary proper. Fishes of the genera *Protammodytes, Bleekeria, Ammodytoides*, and *Lepidammodytes* have a thin, flexible and plate-like pedicel (Figs. 11A, B). The pedicel originates at the symphyseal part of the premaxillary and parallels the vertical axis of the body anteriorly and the dorsal surface posteriorly. Thus the pedicel twists rectangularly at the base of the articular process. While fishes of the genus *Ammodytes* (Figs. 11E, F) have rod-like pedicels which are rather stiff and less flexible. The structure in the genus *Gymnammodytes* (Fig. 11D) is most specialized; the left and right elements are firmly fused and the anterior part of the ascending process is widely broadened and the articulating surface with the premaxillary proper is larger than in other genera. Thus the nature of the pedicel is completely different from the premaxillary proper. *Hyperoplus* (Fig. 11G) lacks upper jaw protrusibility and the pedicel becomes short, but is slightly longer than the articular process of the maxillary.

Another peculiar feature of the jaw structure of the family is that the antero-lateral perforation of the dentary (Figs. 12 A-F). This feature is consistently present throughout the family. This perforation receives the labial ossicles or cartilage when the mouth is closed. In fishes of the genera *Gymnammodytes, Ammodytes*, and *Hyperoplus* the perforation becomes a very narrow slit. Two more derived features can be seen in the anterior part of the dentary: the anteriormost part of the dentary projects downward and is most conspicuous in *Lepidammodytes*, followed by *Gymnammodytes, Bleekeria, Ammodytes, Ammodytoides*, and *Protammodytes* (this projection apparently is to be related to their sand diving behavior); the dentary canal of the lateralis system ends a tiny aperture on a conical elevation situated just behind the anterior projection of the dentary and it is most conspicuous in *Lepidammodytes*; the function of this elevation is not clear.

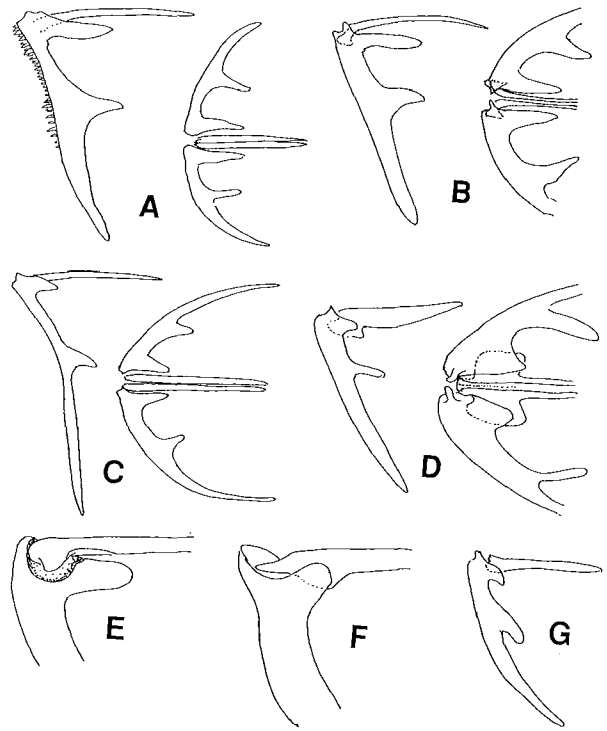

Fig. 11. Upper jaw structure of fishes of the family Ammodytidae (Lateral views, dorsal views are also shown for B, C, and D). Note the difference in the mode of articulation between ascending part and the premaxillary proper. In fishes of genera *Bleekeria* and *Ammodytoides* (A, B) the two elements are fused at medial part of snout but they are connected by a movable articulation in fishes of genera *Ammodytes, Gymnammodytes*, and *Hyperoplus* (D-G). A: *Bleekeria mitsukurii*, B: *Ammodytoides* sp. C: *Lepidammodytes macrophtalmus*, D: *Gymnammodytes cicerelus*, E: *Ammodytes personatus*, F: *Ammodytes hexapterus*, G: *Hyperoplus lanceolatus*.

v) Branchiostegals. All the species of the family *Ammodytidae* invariably have 7 branchiostegals. Five elements are attached to the ceratohyal and the rest are attached to the outer surface of the epihyal.

Gill rakers: The modal count and the range of gill rakers for each species is as follows:

Protammodytes brachistos	8 + 20 = 28
P. sarisa	8 + 23 = 31
Bleekeria mitsukurii	7(6-9) + 19(16-22) = 26(23-28)
B. viridianguilla	6(6-9) + 18(16-22) = 24(23-28)
B. kallolepis	(5-6) + (20-21) = 26
Ammodytoides gilli	6 + (22-23) = (28-29)
A. pylei	7(5-7) + 22(22-23) = 29(28-30)
A. kimurai	6 + (21-23) = (27-29)
A. lucasanus	6(6-7) + 23(22-23) = 29(28-30)

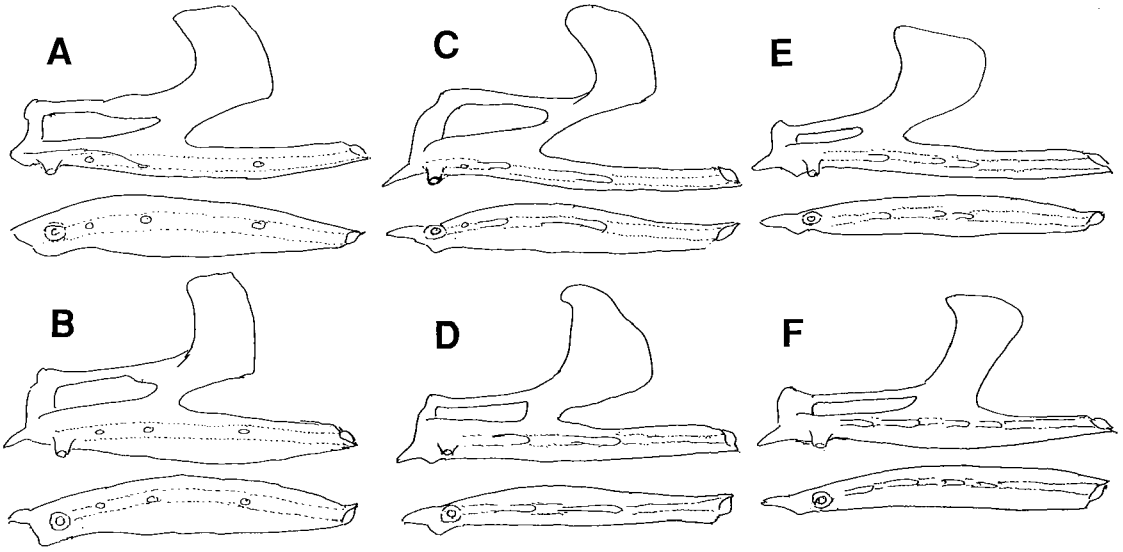

Fig. 12. Dentary of ammodytid fishes. A: *Protammodytes brachistos*, B: *Bleekeria mitsukurii*, C: *Lepidammodytes macrophthalmus*, D: *Ammodytoides pylei*, E: *Ammodytes personatus*, F: *Gymnammodytes cicerelus*. Note the anteroventral projection of dentary in *Lepidammodytes* and openings of mandibular canal are elongated into slits in *Lepidammodytes*, *Ammodytes*, *Ammodytoides*, and *Gymnammodytes*.

A. vagus	6 + (18-20) = (24-26)
A. renniei	6 + (20-21) = (26-27)
Lepidammodytes macrophthalmus	(7-8) + (21-23) = (28-30)
Gymnammodytes capensis	4(4-5) + 20(19-22) = 24(24-27)
G. cicerelus	5(4-6) + 24(23-27) = 29(28-32)
G. semisquamatus	5 + 24 = 29
Ammodytes personatus	5(4-6) + 22(20-24) = 27(25-29)
A. hexapterus	5(4-6) + 21(19-22) = 26(25-27)
A. tobianus	5 + (17-18) = (22-23)
Hyperoplus lanceolatus	5(5-6) + 20(19-20) = 25(24-26)

Thus, the number of gill rakers on the upper limb of the first arch decreases in order from *Protammodytes* (8) to *Lepidammodytes* (8-7), to *Bleekeria* (7,6) and finally *Ammodytes* (5-4). Gill rakers on the lower limb vary from 16 to 27, but usually about 20.

Olfactory organ: The shape and size of the olfactory organ vary greatly within the family and is shown in Fig. 13. In *Protammodytes brachistos* the nasal cavity is situated in the posterior half of the snout and is divided by a thin horizontal wall. The rosette is composed of 10 lamellae above and 9 below, and the whole lamellae occupies about two thirds of the nasal cavity (Fig. 13A). Nostrils lack flaps or any other skin elevation. In *P. sarisa*, the rosette is slightly smaller in size than *P. brachistos* and it is situated in the anterior part of the cavity. The lamellae number four and the whole organ occupies about one-third of the nasal cavity (Fig. 13B). In *Bleekeria mitsukurii, B. vrianguilla*, and *Lepidammodytes* the organ is much smaller than that of *Protammodytes* and it is composed of only four lobes (Figs. 13C, D). The rosette size is very small, extending about half the distance between the two nostrils and occupying less than one sixth of the nasal cavity. In the genus *Ammodytoides*, the olfactory lamella is completely lost (Figs. 13F, G). Instead of the usual lamellae, a foam-like lining of epithelium is developed on the septum just under the anterior nostril, but the nasal cavity itself is much wider than that of *Protammodytes* and *Bleekeria*, extending about three quarters of the snout. No apparent difference is found between *A. lucasanus* (Fig. 13F), *A. pylei* (Fig. 13E), *A. kimurai*, and *A. vagus*. In fishes of the genera *Gymnammodytes, Ammodytes*, and *Hyperoplus*, the foamy lining of epithelium is more developed on the middle of the septum (Figs. 13G-I).

Thus the tendency toward degeneration or specialization of the olfactory organ occurs in the following order: *Protammodytes, Bleekeria, Lepidammodytes, Ammodytoides, Gymnammodytes, Hyperoplus*, and *Ammodytes*.

Caudal fin and its supporting bones: The caudal fin and the last five centra of the family are shown in Fig. 14. The most salient feature of the family in the caudal elements is the number of epurals which number two, contrasting with three epurals in common perciforms. The last two preural haemal spines are autogeneous with their centra

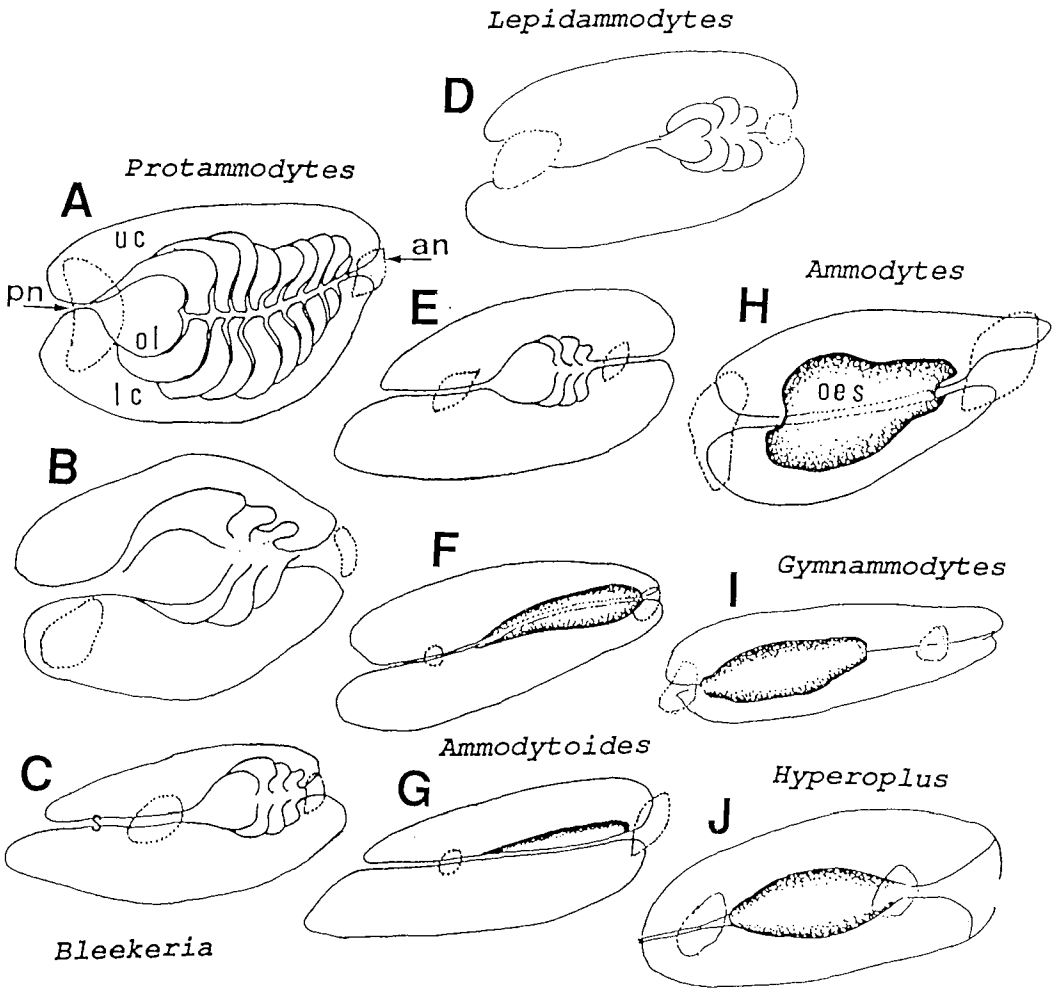

Fig. 13. Olfactory organ (right side) of ammodytid fishes. Dotted lines indicate anterior and posterior nostrils. Note less degenerated state in *Protammodytes* (A, B) and degenerated state in *Bleekeria* (C, E) and *Lepidammodytes* (D), and much modified in other genera (E-I). A: *Protammodytes brachistos*, B: *P. sarisa*, C: *Bleekeria mitsukurii*, D: *Lepidammodytes macrophthalmus*, E: *Bleekeria viridianguilla*, F: *Ammodytoides pylei*, G: *A. lucasanus*, H: *Ammodytes personatus*, I: *Gymnammodytes capensis*, J: *Hyperoplus lanceolatus*.

in the species of four genera, viz. *Protammodytes, Bleekeria, Lepidammodytes*, and *Ammodytoides* (Figs. 14A-G). In species of the genera *Gymnammodytes, Ammodytes*, and *Hyperoplus*, the penultimate haemal spine is fused with the centrum and this tendency is also found in the ultimate spine.

The number of principal caudal rays is consistently 8 + 7 throughout the family. Skeletal elements supporting the caudal fin of ammodytids are as follows: the last 5 to 3 haemal spines, parhypural, the first to 5th hypurals, stegural, two epurals, and the last 2 to 5 neural spines. Except for the number and shape of haemal and neural spines supporting the procurrent caudal rays, little difference can be found between genera of the family. The third and fourth hypurals and the urostyle are fused into a single plate in adults, but these elements are separated at younger stages.

In the genus *Protammodytes*, the upper caudal procurrent rays are 15 or 18, and those of the lower are 16 or 19, and their supporting neural and haemal spines number 4 or 5 and 3 or 4, respectively (Figs. 14A, B). Caudal skeletons of the genus *Bleekeria* are similar to those of *Protammodytes*. But the 2nd epural is smaller than the 1st, and the 5th hypural is thinner than that of the former genus. The upper and lower procurrent rays range from 14 to 17 and 16 to 18, respectively, and their supporting neural and haemal spines range from 3 to 4 and 4 to 5 (Figs. 14C, D).

The number of caudal procurrent rays of *Lepidammodytes* ranges from 16 to 17 (upper) and 15

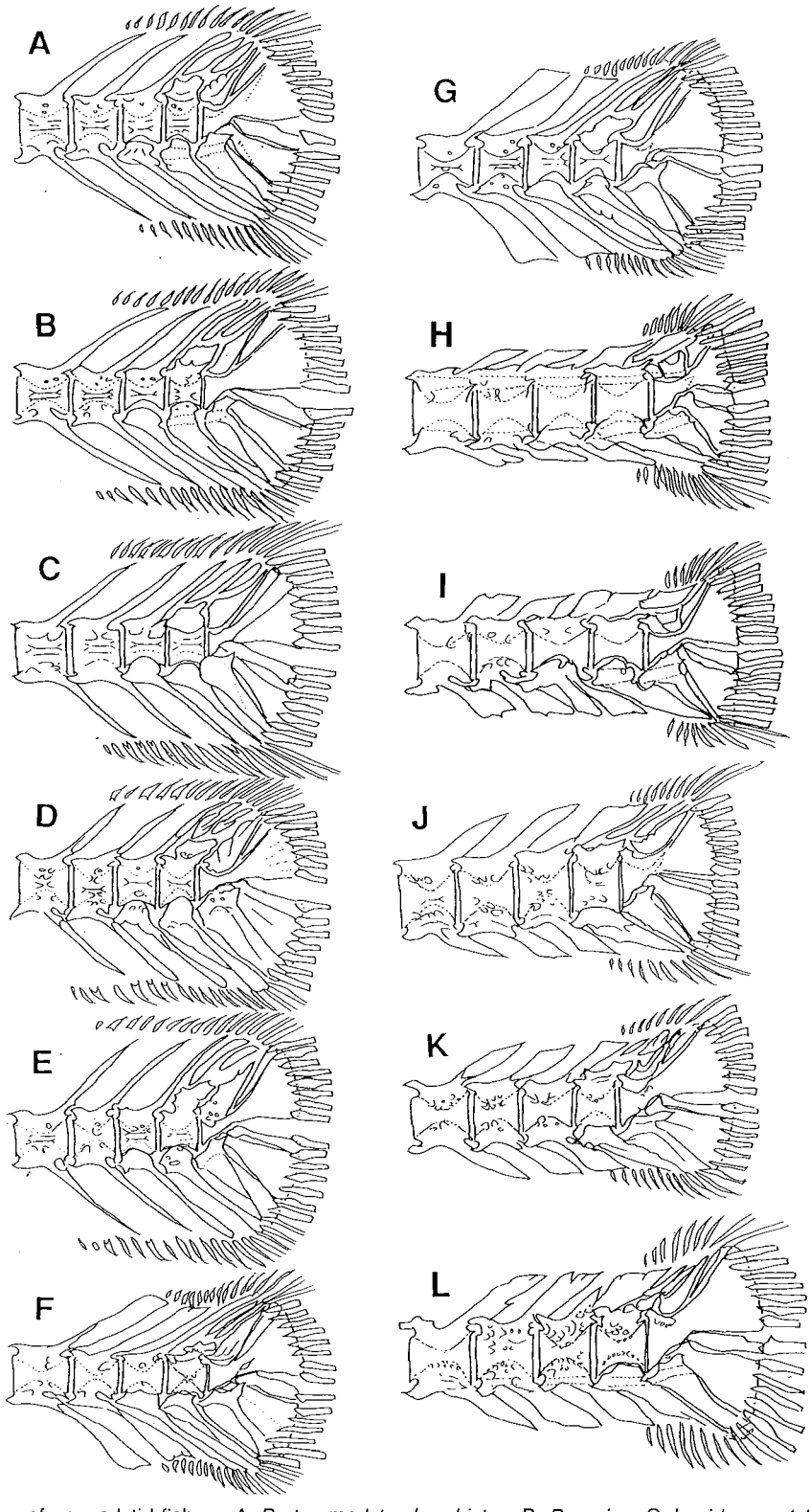

Fig. 14. Caudal skeletons of ammodytid fishes. A: *Protammodytes brachistos*, B: *P. sarisa*, C: *Lepidammodytes macrophthalmus*, D: *Bleekeria mitsukurii*, E: *B. viridianguilla*, F: *Ammodytoides pylei*, G: *A. vagus*, H: *Gymnammodytes cicerelus*, I: *G. capensis*, J: *Ammodytes personatus*, K: *A. hexapterus*, L: *Hyperoplus lanceolatus*. Note the expansion of neural and haemal spines in *Ammodytoides, Gymnammodytes, Ammodytes*, and *Hyperoplus*. Two epurals are fused into a single element in *Gymnammodytes* (H, I). Reduction of depth of caudal vertebrae occurs in the following order: *Protammodytes, Bleekeria, Lepidammodytes, Ammodytoides, Ammodytes, Hyperoplus*, and *Gymnammodytes*, and the number of procurrent caudal rays reducing almost the same order.

to 17 (lower) and their supporting spines number 4 (Fig. 14C).

In the genus *Ammodytoides*, the number of upper and lower procurrent rays range from 14 to 15 and 13 to 14, respectively, and posterior 2 to 3 haemal and neural spines support them. The genus *Ammodytoides* is clearly different in this respect from *Protammodytes, Bleekeria*, and *Lepidammodytes* by having the expanded haemal and neural spines on several posterior caudal vertebrae (Figs. 14F, G). Neither haemal or neural spines of the 2nd preural are not expanded.

The genera *Ammodytes* and *Hyperoplus* show some specialization in their caudal bones, i.e., marked expansion of neural and haemal spines and the gradual fusion of the elements. In a 153 mm SL specimen of *A. tobianus*, the uroneural, five hypurals, and the urostyle are all fused into a single plate. About 10 procurrent caudal rays are present on both the upper and lower bases and are supported only by the last neural spine and epurals dorsally and by the last two haemal spines ventrally (Figs. 14J-L).

The most specialized features can be seen in the genus *Gymnammodytes*. Neural and haemal spines decrease their height and interspaces between the spines are the narrowest among member of the family (Figs. 14H, I). The two epurals in *G. cicerelus* and *G. capensis* are fused into a single broad plate. The number of procurrent rays is less than 11. The rays are supported by the epural dorsally and by the last one or two haemal spines ventrally.

Thus reduction of the procurrent caudal rays occurrs in the following order: *Protammodytes, Bleekeria, Lepidammodytes, Ammodytoides, Ammodytes, Hyperoplus*, and *Gymnammodytes*. The degree of expansion of haemal and neural spines occurrs in the same order.

DISCUSSION

As mentioned in an earlier section, there are very few papers that deal with the detailed morphology of the family Ammodytidae. Jordan (1906) recognized three genera from Japanese waters. Fowler (1953) reported four genera from the waters around China. Duncker and Mohr (1937) revised the family, recognizing the six genera *Bleekeria, Embolichthys, Gymnammodytes, Ammodytes, Hypoptychus*, and *Ammodytoides*. Of these, the genus *Hypoptychus* was placed in the suborder Gasterosteoidei (Ida 1976). Characters used for diagnosis of genus and species were mostly external structures such as squamation, presence or absence of the pelvic fins, ventral skin fold, and other meristic features. Even for these external morphological features, some characters were treated improperly. Dorsal and anal fin rays were regarded as simple (Gosline 1963) but they are divided in the species of *Bleekeria, Protammodytes, Lepidammodytes*, and *Ammodytoides*. Most authors reported that the family lacked dentition (Matsubara 1963, Reay 1986), but teeth are present in the species of *Bleekeria* (Fowler 1953). This point was already established by Robins and Bohlke (1970) and ascertained for *B. kallolepis* by the present authors. The genus *Hyperoplus* had been characterized as having vomerine teeth by many authors (e.g., Duncker and Mohr 1939, Reay 1986). As Kayser (1961) correctly pointed out, they are not teeth but are the anterior hooked ends of the prevomer. Monod (1968) illustrated the caudal skeletons of two species of *Ammodytes*. Fujita (1990) reported the structure of *A. personatus*. Kayser (1961) described the detailed structures of the neurocranium of *Ammodytes tobianus* and *Hyperoplus lanceolatus* in relation to the protrusile jaw mechanism. Gosline (1963) illustrated the pectoral and caudal skeletons of *Ammodytes tobianus* and *Ammodytoides gilli*, discussing the systematic position of *Hypoptychus dybowskii* and showing the perciform attributes of the family Ammodytidae. He also pointed out the presence of unique ossicles in the upper jaw of *A. gilli*. The detailed structure of the ossicles was illustrated by Ida (1973). Pietsch (1984) also discussed the similarity of upper jaw structure in some fishes, together with that of *Ammodytes hexapterus*. McAllister (1968) described the branchiostegal structure of *A. hexapterus*. Recently, Pietsch and Zabetian (1990) clarified the osteology and squamation of *Bleekeria mitsukurii* in detail and compared it with the fishes of some trachinid species such as Cheimarrichthyidae, Pinguipedidae, Trichonotidae etc. and labeled the family Ammodytidae as a sister group of the group consisting of the families Trachinidae and Uranoscopidae.

Most authors have recognized that the family Ammodytidae is not strikingly different from the Perciformes. But none of the authors has treated the whole family. The validity of some genera and species and also their systematic relationships are discussed below.

Systematic relationships of the seven genera of the family Ammodytidae

According to Gosline (1960 1961) and Johnson

Table 3. Counts (mode) and measurements (mean, in hundredth of standard length) of 20 species of the family Ammodytidae

Species	*Protammodytes*		*Bleekeria*			*Ammodytoides*						*Lepidammodytes*	*Gymnammodytes*			*Ammodytes*			*Hyperoplus*	
	br	*sa*	*ka*	*mi*	*vi*	*gi*	*ki*	*lu*	*py*	*re*	*va*	*ma*	*ca*	*ci*	*se*	*he*	*ma*	*pe*	*to*	*la*
number of specimen	2	2	2	43	38	8	6	3	8	2	3	5	11	32	2	45	6	68	5	6
D	36-37	45	37-41	41	42	46	49	46	49	50	48	51	51	55	52	61	61	57	61	59
A	16-17	17	14-16	16	15	23	24	22	24	24	22	19	27	27	29	30	32	30	29	30
P1	16	15	16	15	14	?	15	15	16	?	16	15	14	14	14	14	13	13	12	13
P2	5	5	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Verte.	29+24	33+25	27+25	29+24	29+24	33+23	33+26	32+24	34+26	32+25	33+25	36+26	38+22	39+25	42+25	49+25	41+27	39+24	36+25	40+28
pre/pos D	5/16	4/13	4/13	4/13	4/13	4/11	4/12	4/11	4/12	4/11	4/12	4/12	8/4	8/5	9/5	7/5	7/6	7/5	7/6	8/6
post A	13	13	12	13	12	10	10	10	10	9	9	13	4	4	5	6	6	5	6	6
LL	92	94	99	115	114	105	114	106	121	115	107+5	116	97	107	108	129	127	165	124	170
Ltr	4/13	4/9	4/19	4/19	4/21	3/14	3/15	3/13	3/17	2/15	3/18	3/12	0	0	0	4/32	3/32	4/34	3/28	5/38
Gr	8+20	8+23	5+21	7+20	6+18	6+23	6+22	6+23	7+22	6+21	6+21	7+21	4+20	5+24	5+24	5+21	6+19	5+22	5+17	5+20
Brst expanded	5+2	5+2	5+2	5+2	5+2	5+2	5+2	5+2	5+2	?	5+2	5+2	5+2	5+2	5+2	5+2	5+2	5+2	5+2	5+2
N & H sp	0, 0	0, 0	0, 0	0, 0	0, 0	6, 5	8, 6	6, 6	5, 5	?	7, 6	0, 0	7, 7	6, 7	8, 9	5, 5	7, 7	5, 5	7, 7	6, 5
	20.5	99	103	65	93	83	99	64	158			136	141	94	168	113	148	141	145	259
SL (mm)	-86.0	-117	-106	-139	-124	-116	-129	-117	-173	59-60	54-150	-159	-180	-121	-170	-123	-167	-153	-174	-266
HL (%inSL)	24.5	24.0	23.6	22.7	21.5	23.2	23.0	24.6	22.2	24.9	24.8	22.2	21.9	19.9	20.4	22.7	19.1	20.5	21.1	21.2
ED	4.6	6.1	4.1	4.5	4.7	3.8	3.1	3.4	3.6	5.0	4.6	5.7	3.1	3.2	2.8	4.0	3.2	2.8	3.3	2.2
UJL	8.6	7.7	7.0	6.2	5.98	7.8	7.7	6.9	6.8	7.6	8.8	6.4	6.7	6.6	6.7	7.3	5.8	5.9	6.8	7.1
Snt L	7.5	7.5	6.4	6.1	5.8	5.9	7.1	6.4	6.2	6.8	6.9	6.3	5.9	6.0	5.9	6.8	5.7	5.8	5.9	7.3
BD at Dorg	12.9	10.0	12.6	11.4	13.4	?	10.2	10.3	9.5	10.0	9.9	10.4	10.2	8.6	8.0	9.2	8.6	10.0	9.6	7.6
at Aorg	10.0	9.5	11.0	11.3	14.0	9.7	10.3	10.2	10.1	10.0	10.0	10.5	10.2	9.2	7.2	8.8	7.8	9.4	8.3	7.7
CPD	7.0	5.3	6.7	6.2	7.2	5.8	4.7	5.3	4.3	5.4	4.7	5.39	3.4	2.5	2.3	3.1	3.1	2.8	3.4	3.0
P1FL	10.8	12.0	13.6	12.9	13.4	?	9.2	8.9	8.8	?	9.3	12.1	9.8	8.1	8.5	11.3	9.9	9.6	10.5	7.3
P2FL	7.7	7.6	5.9	0	0	0	0	0	0	0	0	3.42	0	0	0	0	0	0	0	0
Snt-Dorg	30.7	25.5	23.2	23.1	22.5	24.2	24.1	25.8	22.1	25.5	25.2	23.5	31.2	27.5	30.0	29.0	24.8	26.1	28.5	27.2
Snt-P1	24.3	22.5	21.7	20.8	21.6	21.5	22.6	23.0	19.5	23.2	23.2	21.7	21.1	18.3	19.4	22.0	18.2	19.0	20.1	20.9
Snt-Anus	61.5	57.5	61.8	62.9	62.6	62.9	63.2	62.9	64.0	63.6	65.5	68.9	66.2	64.1	64.0	65.2	61.8	61.5	63.1	61.9
D base	51.9	57.5	61.9	60.2	61.2	29.8	65.2	63.2	63.2	62.2	62.4	62.2	68.4	69.9	66.2	69.4	69.8	69.7	70.2	69.0
A base	19.0	17.0	20.0	19.8	19.4	24.1	25.9	25.0	23.0	24.3	24.6	17.9	29.7	31.4	30.0	30.1	32.7	32.6	32.6	31.9

Species abbreviations. *br: Protammodytes brachistos, sa: P. sarisa, ka: Bleekeria kallolepis, mi: B. mitsukurii, vi: B. viridianguilla, gi: Ammodytoides gilli, ki: A. kimurai, lu: A. lucasanus, py: A. pylei, re: A. renniei, va: A. vagus, ma: Lepidammodytes macrophthalmus, ca: Gymnammodytes capensis, ci: G. cicerelus, se: G. semisquamatus, he: Ammodytes hexapterus, ma: A. marinus, pe: A. personatus, to: A. tobianus, la: Hyperoplus lanceolatus.*

(1984) the attributes of the Perciformes are summarized as follows. The pelvic fin consists of one spine and five rays, principal caudal rays are 9+8, the pelvic girdle is attached to the cleithrum, five infraorbitals are present behind the lachrimal, orbitosphenoid, antorbital, and nodules between the pelvic fin rays and its girdle are absent, two postcleithra are present, the last two haemal spines are autogeneous with centra, the second suborbital does not form a stay for the preopercle.

Added to the above mentioned characters are the presence of spines on dorsal and anal fins, vertebral composition less difference from 10 + 14 (totaling 24) and the presence of ctenoid scales. These features may be regarded as primitive or generalized conditions as a member of Perciformes.

The family Ammodytidae shares with other perciforms pelvic girdle structure and number of postcleithra, the five infraorbital (six including lachrimal *Protammodytes* only), and state of the second infraorbital. On the other hand, the family has many unique derived characters such as an elongated body, with abdominal vertebrae being in number than that of the caudal, absence of fin spines, a perforation on the dentary, presence of pelvic spur, a scale arrangement forming diagonal straight lines, reduced principal caudal rays, and two epurals instead of three. According to Pietsch and Zabetian (1990), some of these characters are shared with the trachinoids. But it may be noted here that in their cladogram, 10 characters of the family out of 26 characters they used, are not shared. The family Ammodytidae differs strikingly in the following characters from the trachinoids: (derived state) the number of abdominal vertebrae being greater than those of the caudal, the number of epural is two instead of three, the hypural plates number three and four and are always fused together, the dentary has an anterodorsal perforation, the dentary also has an anteroventral projection probably related to sand diving behavior; (generalized state) principal caudal rays invariably number 8+7 (less than this count excluding Mugiloididae and Chiasmodontidae).

Thus, the family exhibits a very complicated or mosaic character states, both in generalized and much derived features. Counts (range or mode) and measurements (mean) of 20 species of the family Ammodytidae are shown in Table 3. If a typical perciform fish were chosen as an out-group of the family, then its complex of characters is summarized in Table 4.

In order to clarify the relationships of genera of the family, relationships of the seven genera were analyzed with the Wagner parsimony method and Fitch method based algorithm using 27 character states. Of the 14 trees drawn by their methods the following tree seems the most plausible (Fig. 15).

Table 4. Summary of character state of the family Ammodytidae

Character	Generalized	Derived
abdominal vertebra	less than 36	more than 37
anal fin rays	less than 25	more than 26
dorsal fin rays	less than 44	more than 45
fin branching*	present	absent
predorsal bone*	present, 2	absent
ventral skin fold*	absent	present
infraorbitals	complete	incomplete
pelvic fin*	present	absent
pectoral girdle	high, thin	low, thick
prc. c. ray	more than 17	less than 15
predorsal vert.	less than 5	more than 7
postdorsal v.	more than 11	less than 6
lacrimal	short, high	long, low
lateral line	less than 110	more than 120
labial ossicle*	absent	present
scale*	present	absent
dermal plicae	absent	present
olfactory organ	lobes present	lobes absent
premaxillary	asp thin	asp bold
dentary, coronoid prc	narrow	wide
epurals	long, not fused	short, fused
last two h. sp.*	autogeneous	fused with entra
caudal h. & n. spines*	not expanded	expanded
prevomer*	not protruded	protruded from roof
dentition*	present	absent
opercular scale*	present	absent
squamation*	not embedded	embedded

Characters without an asterisk were analyzed by Wagner's method and those with an asterisk were analysed by algorithm based on Fitch.

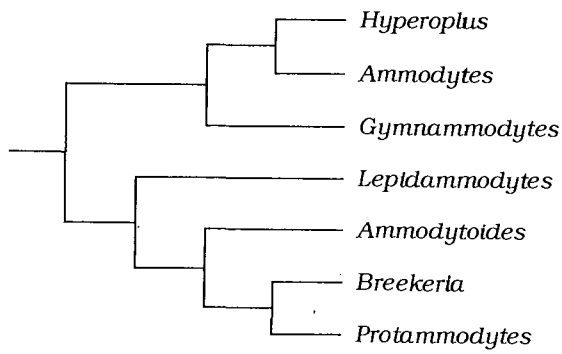

Fig. 15. Cladograms showing phylogenetic relationships of the seven genera of the family Ammodytidae. Cladogram based on Wagner/Fitch method.

It seems clear that the family is split into two groups. The first group having less specialized characters includes *Protammodytes, Bleekeria, Lepidammodytes*, and *Ammodytoides*. The second group which has many specialized characters includes *Gymnammodytes, Ammodytes*, and *Hyperoplus*. The first group may be called Bleekeriinae and the second group, Ammodytinae. In Bleekeriinae, *Protammodytes* and *Bleekeria* show many generalized features such as the absence of labial ossicles and lateral plicae, neural and haemal spines of caudal vertebrae not expanded, presence of usual olfactory lobes and of the two predorsals, and the lateral line system continuous on the head with that on the body. Thus these two genera show closest affinity among members of the subfamily. The *Ammodytoides* show slightly advanced or specialized characters. The genus *Lepidammodytes* is unique in having a mosaic set of characters: ctenoid scales, presence of pelvic fins, branching of most rays of dorsal and anal fins as a generalized feature and an elongated body, with perforation in the lachrimal as a derived state.

In Ammodytinae, the three genera share many specialized features such as expanded neural and haemal spines of caudal vertebrae, fusion of the penultimate haemal spine with the centrum, lateralis systems not continuous between head and body, reduction of procurrent caudal rays, reduction of the infraorbitals (about half of them are lost), and absence of the predorsals. Of these genera, *Gymnammodytes* exhibits the most specialized state in many characters, while the genera *Ammodytes* and *Hyperoplus* share the characters of absence of labial ossicles, developed lateral plicae and fine scales deeply embedded in the plicae. One of the most salient aspects of the subfamily, excluding *Gymnammodytes*, is the scale arrangement forming diagonal straight lines and scales embedded in the dermal plicae. These specializations occur together with the elongation of the body mainly by the increment of abdominal vertebrae.

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玉筋魚科魚類形態之比較研究兼記兩新屬新種之玉筋魚

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本文主要在檢討玉筋魚科魚類屬的特徵，同時並描述兩個新屬及新種之玉筋魚類。其中*Protammodytes*新屬(模式種：*Protammodytes branchistos*)之特徵爲具臀鰭、鱗片非向後下方斜向排列，脊椎骨數較少，眶下骨系列完整。這些特徵可能是本科最原始的特徵。另一新屬是*Lepidammodytes*(模式種：*Lepidammodytes macrophthalmus*)之特徵爲具強櫛鱗，眼較大，淚骨有孔，脊椎骨數目適中；其一般及進化形質之組合情形在本科魚類獨具一格。

玉筋魚之*Bleekeria* Gunther屬應分成兩個屬，即*Bleekeria* Gunther及*Ammodytoides* Duncker and Mohr。其中*Bleekeria*屬包括*B. kallolepis*; *B. mitsukurii*；及*B. viridianguilla*三種；*Ammodytoides*屬包括*A. gilli, A. vagus, A. renniei, A. lucasanus, A. kimurai*，及*A. pyiei*等六種；其特徵爲具唇小骨(labial ossicle)，腰帶無鰭，尾椎後段之神經棘及血道棘擴大，無側皮褶。Embolichthys現置於*Bleekeria*屬下，成爲一亞屬層級。

本科之七個屬又可歸成兩亞科，即Bleekeriinae及Ammodytinae。Bleekeriinae亞科含*Protammodytes, Bleekeria, Lepidammodytes*，及*Ammodytoides*等四屬。Ammodytinae亞科包含*Gymammodytes, Ammodytes*及*Hyperoplus*等三屬。Bleekeriinae亞科具有許多一般性形質，Ammodytinae亞科具有許多進化形質，*Ammodytoides*及*Gymnammodytes*二屬之形質類型則恰好介於上述一般及進化型兩亞科之間。

關鍵詞：玉筋魚科，形態，新屬，魚類分類。

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