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Subgenera of *Enoploteuthis*, *Abralia* and *Abraliopsis* of the Squid Family Enoploteuthidae (Cephalopoda, Oegopsida)

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Abstract The subgenera in three genera of oegopsid squid family Enoploteuthidae (*Enoploteuthis*, *Abralia* and *Abraliopsis*) are revised. The genus *Enoploteuthis* contains two subgenera, *Enoploteuthis* s. str. and *Paraenoploteuthis* nov. The former subgeneric arrangement of the genus *Abralia* is changed. It is divisible into five subgenera, namely, *Abralia* s. str., *Astrabralia*, *Asteroteuthis*, *Pygmabralia*, and *Heterabralia* nov. The genus *Abraliopsis* consists of four subgenera, *Abraliopsis* s. str., *Micrabralia*, *Boreabraliopsis* nov., and *Pfefferiteuthis* nov. Relationships among genera and subgenera of the family are discussed.

Several subgenera of the Family Enoploteuthidae have been proposed since earlier studies of PFEFFER (1900, 1912) and CHUN (1900), and recently by NESIS (1987). During the course of the extensive taxonomic studies on the enoploteuthid squids, mainly from the North Pacific, it became clear that the genera *Enoploteuthis*, *Abralia* and *Abraliopsis* are reasonably divisible into subgenera or at least species-groups that are critically revised here. Those subgeneric names are chronologically arranged in the following lines.

The genera *Watasenia* ISHIKAWA, 1913, and *Enigmoteuthis* ADAM, 1973 were established by monotypy, and they are not necessary to be revised herewith.

I. Subgenera of the Genus *Enoploteuthis*

The grouping of the species in the genus *Enoploteuthis* seems to have first been attempted by ROPER (1966). Later, BURGESS (1982) recognized the two species-groups, *leptura*-complex and *anapsis*-complex, based on the tentacular characters, such as the degree of prominency of club, the size of manus hooks, the dactylus sucker arrangement, and the shape of carpus. The more critical definition is given here basically to follow BURGESS's scheme (Table 1).

1. Subgenus ***Enoploteuthis*** D'ORBIGNY, 1848 (s. str.)

Type species: *Loligo leptura* LEACH, 1817.

Diagnosis: Body is rather large. Right ventral arm of the male is hectocotylized. Hectocotylus is composed of a single ventral flap. Many small papillae are present on

Table 1. An abridged comparison of selected criteria of two subgenera of the genus *Enoploteuthis*.

	Enoploteuthis s. s.	*Paraenoploteuthis* nov.
Oral surface of arms	Papillated	Normal
Hectocotylization	1 flap	2 flaps
Tentacle:		
Club	Very narrow	Expanded
Carpal group	Elongate	Discoidal
Manus hooks	Subequal in size	Unequal in size
Dactylus suckers	2 rows	4 rows
Ventral flap	Absent	Present

the oral surfaces of the Arms I–III. Tentacle is short and weak. Ventral flap of the tentacle is absent. Fixing apparatus is elongate. Ventral hooks of manus are slightly larger than the dorsal hooks. Dactylus suckers are arranged in two longitudinal rows (Figs. 1–3).

Included species:

1. *Enoploteuthis leptura* (LEACH, 1817)
2. *Enoploteuthis reticulata* RANCUREL, 1970
3. *Enoploteuthis obliqua* BURGESS, 1982
4. *Enoploteuthis octolineata* BURGESS, 1982.

Geographical distribution: Warm waters of the world.

Remarks: This subgenus is easily separable from the other in having biserial dactylus sucker rows. The conical small papillae on the oral surfaces of the Arms I-III of *E. leptura* mentioned by ROPER (1966) are also present in the Pacific species, *E. reticulata*, *E. obliqua* and *E. octolineata*.

2. Subgenus ***Paraenoploteuthis*** nov.

Type species: *Enoploteuthis chuni* ISHIKAWA, 1914.

Disagnosis: Right ventral arm of the male is hectocotylized. In the hectocotylized arm, a pair of different sized, offset crests are prominent, of which the distal one is situated on the dorsal margin and proximal one, on the ventral margin of the oral surface of the arm. Tentacle is long and robust. The ventral flap of tentacle is present. Fixing apparatus is oval in shape. Ventral hooks of the manus are larger than the dorsal hooks. Dactylus suckers are arranged in four longitudinal rows (Figs. 4–5).

Included species:

1. *Enoploteuthis chuni* ISHIKAWA, 1914
   syn. *E. theragrae* TAKI, 1964
2. *Enoploteuthis galaxias* BERRY, 1918
3. *Enoploteuthis anapsis* ROPER, 1964
4. *Enoploteuthis jonesi* BURGESS, 1982
5. *Enoploteuthis higginsi* BURGESS, 1982.

Figs. 1–3. *Enoploteuthis* (s.s.) *reticulata* RANCUREL, 1970, male (99.1 mm DML) from Uraga Channel, 700 m wire paid-out (*Soyo-Maru*, 1957). —— 1. Left Arm I. 2. Right tentacle. 3. Hectocotylized arm.

Figs. 4–5. *Enoploteuthis* (*Paraenoploteuthis* nov.) *chuni* ISHIKAWA, 1914, male (76.7 mm DML) from 30°04.6′ N, 134°27.9′E, 530–560 m (*Kaiyo-Maru*, 1986). —— 4. Right tentacle. 5. Hectocotylized arm, oral and lateral views. [Scale bars: 5 mm.]

Geographical distribution: Warm to cool temperate waters of the Atlantic and Pacific.

Remarks: On the evaluation of the characters to split the genus *Enoploteuthis*, BURGESS (1982) considered that the presence or absence of the ventral flap of the carpus is one of the important criteria. RIDDELL (1985) described the presence of the ventral flap in *E. galaxias* from New Zealand waters. The papillation on the oral surfaces of arms characterizing the subgenus *Enoploteuthis* is not present in this subgenus.

II. Subgenera of the Genus *Abralia*

The subgenera of the genus *Abralia* were studied by several authors (PFEFFER, 1900, 1912; GRIMPE, 1931; VOSS, 1954, 1963; CLARKE, 1966; NESIS, 1982). The recent discoveries of several new species from the Indian Ocean (OKUTANI, 1983),

Table 2. An abridged comparison of selected criteria of five subgenera of the genus *Abralia*.

	Abralia s. s.	*Astero-teuthis*	*Astr-abralia*	*Pygm-abralia*	*Heter-abralia* nov.
Arm terminal sucker rows	3–4	3–4	2	2	2
Hectocotylization (arm IV)	Right	Left	Right	Right	Left
Tentacular hooks	≧5	≦4	≧5	≦4	≦4
Subocular photophores	2 types	2 types	1 type	1 type	2 types
Caudal photophores	Absent	Absent	Present	Absent	Absent

Table 3. Relationships among nominal subgenera of *Abralia* in the previous authors and the present study.

GRIMPE (1931) & NESIS (1980)	NESIS (1987)	Present study
Abralia	*Abralia*	*Abralia*
	Stenabralia	
Stenabralia	*Astrabralia*	*Astrabralia*
Asteroteuthis	*Asteroteuthis*	*Asteroteuthis*
		Heterabralia nov.
	Pygmabralia	*Pygmabralia*
	Arabralia	

the Atlantic (LIPIŃSKI, 1983), and the Pacific (VOSS, 1963; OKUTANI & TSUCHIYA, 1987), as well as the present critical revision led a conclusion that the genus is divisible into five subgenera (Table 2). NESIS (1987) recently proposed a new system with six subgenera which is to some degree different from ours. The change of the subgenera from the previous works is summarized in Table 3.

1. Subgenus ***Abralia*** GRAY, 1849 (s. str.) emend.

Synonym: *Stenabralia* GRIMPE, 1931 (pars.).

Type species: *Onychoteuthis armata* QUOY et GAIMARD, 1832.

Diagnosis: Body is medium to large for the genus. Suckers of the distal portion of the Arms I–III are tri- or quadriserial in adult. Right ventral arm of the male is hectocotylized. Tentacular hooks are more than five in number. Subocular photophores are composed of ovoid, orange-colored mesial organs and elongate, opaque terminal ones (Figs. 6–8).

Included species:

1. *Abralia armata* (QUOY et GAIMARD, 1832)
2. *Abralia steindachneri* WEINDL, 1912
3. *Abralia multihamata* SASAKI, 1929
   syn. *A. lucens* VOSS, 1963
4. *Abralia renschi* GRIMPE, 1931

5. *Abralia spaercki* GRIMPE, 1931
syn. *A. armata* sensu VOSS, 1963.

Geographical distribution: Indo-Pacific.

Remarks: *Abralia armata* (QUOY et GAIMARD, 1832), was described based on a single young specimen from Celebes, and its original description was so short that the taxonomic characters were not satisfactorily understood. Later, VOSS (1963) re-described *A. armata* based on the specimens identified by GRIMPE (1931) from the Philippines. According to QUOY and GAIMARD (1832), *A. armata* is characterized in having six tentacular hooks and biserial rows of distal arm suckers. The holotype specimen of *A. armata* in the Muséum National d'Histoire Naturelle, Paris, is only a gladius (P. BOUCHET, pers. comm.).

GRAY (1849) established the genus *Abralia* based on *Onychoteuthis armata*. GRIMPE (1931) created the subgenus *Stenabralia* in the genus *Abralia*, and species with more than four tentacular hooks were allocated therein. GRIMPE (1931) and CLARKE (1966) considered that the subgenus *Stenabralia* contains six species, namely, *A. astrolineata* BERRY, 1914, *A. astrosticta* BERRY, 1919, *A. lucens* VOSS, 1963, *A. renschi* GRIMPE, 1931, *A. spaercki* GRIMPE, 1931, and *A. steindachneri* WEINDL, 1912.

Among them, *Abralia astrolineata* BERRY, 1914, and *Abralia astrosticta* BERRY, 1909, are readily separable from *A. armata* in having the characteristic terminal photophores on the Arm IV in young stage, and from the other species of *Stenabralia* in having only five monotypic subocular photophores without opaque terminal organs. These two species should be placed in the other subgenus.

Abralia renschi GRIMPE, 1931, is a medium-sized species characterized in having five to seven tentacular hooks and two types of six subocular photophores. This species is easily separable from *A. armata* by the distinctly and regularly longitudinal arrangement of photophores on the mantle.

Abralia steindachneri WEINDL, 1912, and *Abralia lucens* VOSS, 1963, are large-sized species characterized in having five to six tentacular hooks and two types of six to eight subocular photophores, and tri- or quadriserial rows of distal arm suckers.

Abralia spaercki GRIMPE, 1931, was first allocated in the subgenus *Abralia* s. str. by GRIMPE (1931), but later, VOSS (1963) moved it to the subgenus *Stenabralia*. It is characterized by having six to seven tentacular hooks, two types of six to eight subocular photophores, and tri- or quadriserial rows of distal arm suckers. It is separable from the other species by possession of a pair of peculiar photophores in the funnel groove.

Abralia armata sensu VOSS, 1963, has six tentacular hooks, two types of five to seven subocular photophores, biserial sucker rows at the distal tip of the Arms I–III and large "photogenic organ" on the ventral surface of the ink-sac. VOSS described this organ that "the sac is broadly oval and black, but extending across the ventral surface and up the sides laterally is a distinctly demarcated bronze and pearly iridescent layer which appears to be similar to the luminous light organs found on the ink-sac in some other groups." It means that this organ is neither granular nor lens-bearing.

Such an iridescent layer overlying the intestine is commonly observed in young stages of several forms of *Abralia*, as well as other families, such as Cranchiidae. This fact suggests that *A. armata* observed by VOSS (1963) was a young stage. This assumption may be corroborated by the facts that his specimens had a short and plump mantle, indistinct nuchal crests, premature carpus, and weak, slender and elongate arms. These are all characters usually observed in young enoploteuthids. A specimen illustrated by VOSS (Figure 18a) has three pairs of photophores on the dorsal surface of fins. This character suggests that his specimens were most probably young specimens of *A. spaercki*. A peculiar photophore in the funnel groove seem to be overlooked by him.

A Formosan species, *Abralia multihamata* SASAKI, 1929, is characterized by six to seven tentacular hooks, two types of six subocular photophores, and biserial rows of distal arm suckers. The peculiar photophores in the funnel groove are not recognized by SASAKI (1929, text-fig. 173B). It suggests that *A. multihamata* is probably a young stage of *A. lucens*. The photophores on the dorsal fins were never described by SASAKI (1929) and not able to be compared with *A. lucens*.

Therefore, it is assumed that the species hitherto being included in the subgenus *Abralia*, viz. *A. armata* and *A. multihamata*, represent young specimens of the species that have hitherto been assigned to *Stenabralia*. A definition of the subgenus *Stenabralia* given by GRIMPE (1931) is only that *Abralia* with a narrow fin and more than four tentacular hooks. *Abralia* GRAY, 1849, has a priority to *Stenabralia* GRIMPE, 1931, which is thus synonymous with the former. Although GRIMPE (1931) considered that *A.* (*Abralia*) *multihamata* is conspecific with *A. armata*. NESIS (1987) placed it in the subgenus *Asteroteuthis*.

2. Subgenus ***Asteroteuthis*** PFEFFER, 1908

Type species: *Abralia veranyi* (RÜPPELL, 1844).

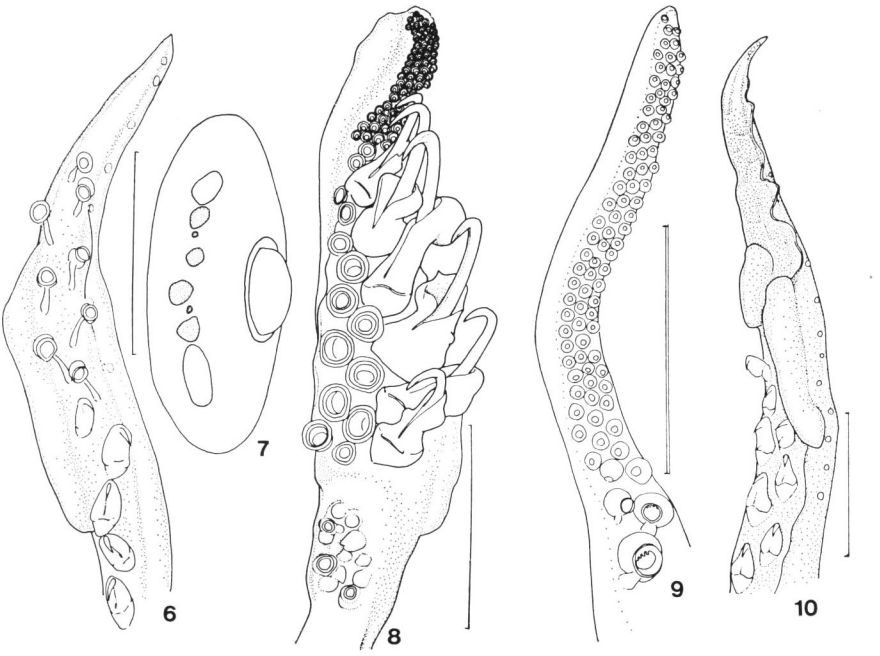
Diagnosis: Body is medium in size. Suckers of the distal portion of the Arms I–III are tri- or quadriserial. Left ventral arm of the male is hectocotylized. Tentacular hooks are three to five in number. Subocular photophores are composed of ovoid, orange-colored mesial organs and elongate, opaque terminal ones (Figs. 9–10).

Included species:

1. *Abralia veranyi* (RÜPPELL, 1844).

Geographical distribution: Atlantic.

Remarks: GRIMPE (1931) allocated *Abralia japonica* ISHIKAWA, 1929, in the subgenus *Asteroteuthis*. *A. japonica* is believed to be a large-sized species characterized by having two large tentacular hooks, three small carpal suckers, and five monotypic subocular photophores, and this is known by only two females from the type locality, Uwozu, Toyama Bay, Japan Sea (ISHIKAWA, 1929). ISHIKAWA (1929) identified this species to be the genus *Abralia* based on the possessions of uniserial hooks on the tentacular club and absence of terminal photophores at the tip of the Arm IV. However, he described that "the buccal membrane deep violet" and, "all these arms bear



Figs. 6–7. *Abralia* (s. s.) *multihamata* SASAKI, 1929. —— 6. Male (38.5 mm DML) from the East China Sea, immature hectocotylized arm (*Yoko-Maru*). 7. Female (28.8 mm DML) from Suruga Bay, 10 m deep, right eyeball (NSMT-Mo 62339).

Fig. 8. *Abralia* (s. s.) *spaercki* GRIMPE, 1931, female (56.0 mm DML) from 27°13.2′S, 153°52.6′E, 500–540 m, left tentacle (NMV F51777).

Figs. 9–10. *Abralia* (*Asteroteuthis*) *veranyi* (RÜPPELL, 1844), male (36.3 mm DML) from 7°40′N, 54°12′W, 402 m deep (NSMT-Mo 61080). —— 9. Distal part of the left Arm I. 10. Hectocotylized arm. [Scale bars: 5 mm (simple) or 2 mm (double).]

small stout hooks in two alternating rows, replaced by some two series of suckers at the extremity, except on the tip of the ventral arm." These two characters never match with those of the genus *Abralia*. Very small carpal sucker and absence of sucker on the Arm IV are characters of genera *Watasenia* and *Abraliopsis*, although two characters, namely, the absence of carpal flap and the absence of terminal photophores on the Arm IV contrarily do not match with both genera. Although ISHIKAWA (1929) mentioned the terminal photophores that "this absence of the organ is neither to be looked upon as the result of an accident nor as due to a secondary of ontogenetic circumstance," the absence of terminal photophores will be due to malformation or artificial defect. The carpal flap is often unnoticed. Also none of specimen has been re-discovered since the original description, in spite of the fact that more than several thousands of *Watasenia scintillans* have hitherto been examined by many previous authors through a long history of fishery biological investigations on this squid and by ourselves for the present study. We consider *Abralia japonica* to be

an abnormal specimen of *Watasenia scintillans*.

3. Subgenus *Astrabralia* NESIS, 1987

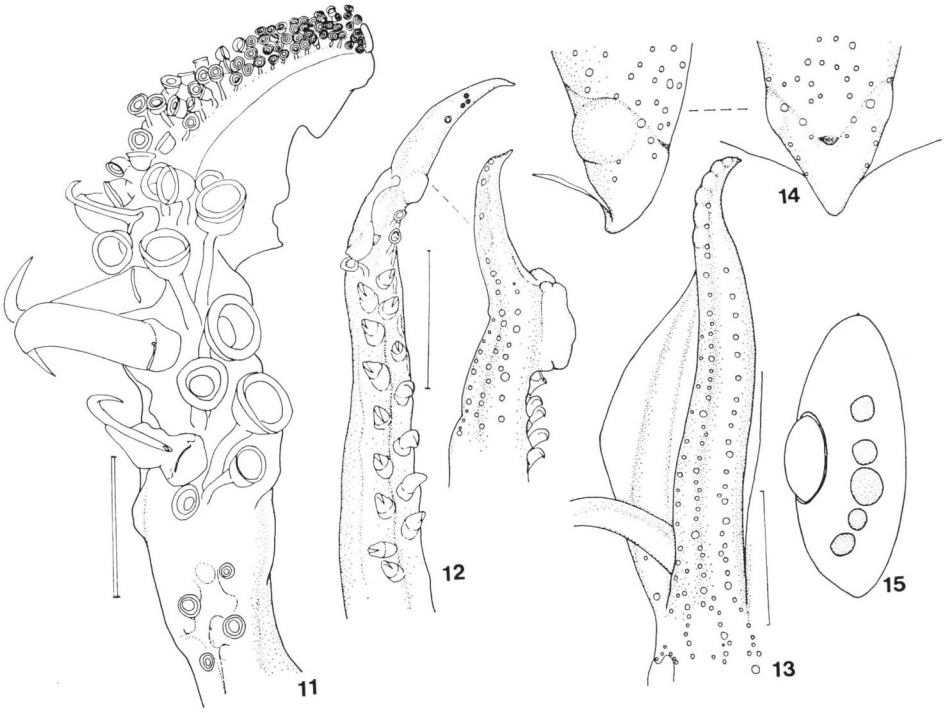
Synonyms:

Compsoteuthis, PFEFFER, 1912 (pars.)

Stenabralia GRIMPE, 1931 (pars.).

Type species: *Abralia astrosticta* BERRY, 1909.

Diagnosis: Body is large. Suckers of the distal portion of the Arms I–III are biserial. Right ventral arm of the male is hectocotylized with a slightly bilobed proximal crest and a lunate distal crest. On the terminal portion of the Arm IV is a row of large hemispherical photophores. A pair of photophores is embedded on the lateral sides of the tail. Tentacular hooks is more than five in number. Subocular photophores are composed of only ovoid orange-colored monotypic organs without elongate



Figs. 11–12. *Abralia* (*Astrabralia*) *astrosticta* BERRY, 1909, male (46.0 mm DML) from 21°36.5′ N, 158°11.5′W, 58 fms. (USNM 730628). —— 11. Right tentacle. 12. Hectocotylized arm, oral and lateral views.

Figs. 13–15. *Abralia* (*Astrabralia*) *astrosticta* BERRY, 1909, young female (41.1 mm DML) from 32°47.3′N, 147°58.7′E, 0–120 m (*Kaiyo-Maru*, 1987). —— 13. Right arm IV, aboral view. 14. Caudal photophores, lateral and ventral views. 15. Right eyeball. [Scale bars: 5 mm (simple) or 2 mm (double).]

opaque one. Photophores on the mantle is arranged in regular rows (Figs. 11–15).

Included species:

1. *Abralia astrosticta* BERRY, 1909
2. *Abralia astrolineata* BERRY, 1914.

Geographical distribution: Pacific.

Remarks: This subgenus is easily separable from the other subgenera by the presence of a row of the large terminal photophores on the Arm IV, which are probably homologous with the photophores in the genera *Abraliopsis* and *Watasenia*, though these terminal photophores are neither swollen nor pigmented unlike terminal organs of those genera.

VOSS (1955) regarded the subgenus *Compsoteuthis* as an invalid name because terminal photophores were not mentioned by PFEFFER (1912) and BERRY (1914b), nor present in a mature specimen (57.0 mm DML) in VOSS's collection. These terminal photophores become indistinct with growth. (They are drawn as the white tubercles in BERRY, 1914b, pl. 51, fig. 1). Another species included in the present subgenus, *Abralia astrolineata* has the same organs which are distinct in young stage (RIDDELL, 1985).

4. Subgenus ***Pygmabralia*** NESIS, 1987

Type species: *Abralia redfieldi* VOSS, 1955.

Diagnosis: Body is small to medium. Suckers of the distal portion of the Arms I-III are biserial. Right ventral arm of the male is hectocotylized with a bilobed proximal flap. Number of tentacular hooks is less than four. Subocular photophores are composed of only ovoid, orange-colored monotypic organs without elongate opaque one (Figs. 19–21).

Included species:

1. *Abralia redfieldi* VOSS, 1955
2. *Abralia grimpei* VOSS, 1958
3. *Abralia marisarabica* OKUTANI, 1983
4. *Abralia similis* OKUTANI et TSUCHIYA, 1987.

Geographical distribution: Atlantic and Indo-Pacific.

Remarks: This subgenus is very close to the subgenera *Asteroteuthis* and *Heterabralia* nov. in the body proportion and the number of tentacular hooks, but distinguishable from them by the right ventral arm hectocotylized. It is also different from them in having a bilobed proximal crest in the modified portion of hectocotylized arm and absence of any elongated opaque terminal subocular photophores.

This subgenus is also distinguishable from the subgenus *Abralia* s. str. in having only the monotypic subocular photophores and biserial arm sucker arrangement.

NESIS (1987) established the subgenus *Arabralia* based on *A. marisarabica*, while it cannot be splitted from the present subgenus by the characters of terminal suckers of the arms, morphology of hectocotylized arm, number of tentacular hooks, and composition of subocular photophores.

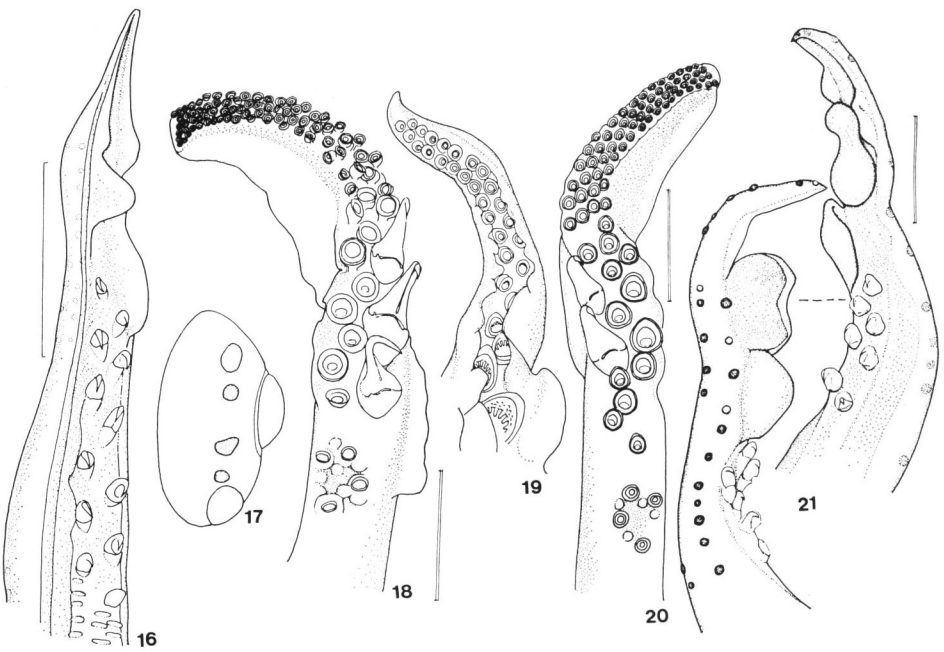
Abralia grimpei VOSS, 1958, was classified by NESIS (1983, 1987) into the subgenus *Asteroteuthis*, while it should be transferred to the present subgenus because of having monotypic subocular photophores.

5. Subgenus ***Heterabralia*** nov.

Synonym: *Asteroteuthis* PFEFFER, 1908 (pars.).

Type species: *Abralia andamanica* GOODRICH, 1896.

Diagnosis: Body is medium in size. Suckers of the distal portion of the Arms I–III are biserial. Left ventral arm of the male is hectocotylized. Tentacular hooks are less than four in number. Subocular photophores are composed of ovoid, orange-colored mesial organs and elongate, opaque terminal ones (Figs. 16–18).



Figs. 16–18. *Abralia* (*Heterabralia*, nov.) *robsoni* GRIMPE, 1931. —— 16. Male (38.0 mm DML) from the East China Sea, 0–310 m, hectocotylized arm (*Yoko-Maru*). 17, Female (48.2 mm DM) from off Odawara, Sagami Bay, left eyeball (*Soyo-Maru*, 1973). 18. Female (49.0 mm DML) from off Odawara, Sagami Bay, left tentacle (*Soyo-Maru*, 1973).

Figs. 19–21. *Abralia* (*Pygmabralia*) *similis* OKUTANI et TSUCHIYA, 1987. —— 19. Female (32.4 mm DML) from 30°04.6′N, 134°27.9′E, 0–560 m, distal portion of the Arm II (NSMT-Mo 66645). 20. Male (18.6 mm DML) from 30°03.2′N, 134°03.5′E, 0–550 m, right tentacle (NSMT-Mo 66642: Holotype). 21. Male (17.7 mm DML) from 30°04.5′N, 143°46.6′E, 500–900 m, hectocotylized arm, two different views (NSMT-Mo 66644). [Scale bars: 5 mm (simple) or 2 mm (double).]

Included species:

1. *Abralia andamanica* GOODRICH, 1896
2. *Abralia trigonura* BERRY, 1913
3. *Abralia robsoni* GRIMPE, 1931
4. *Abralia siedleckyi* LIPIŃSKI, 1983.

Geographical distribution: Indo-Pacific.

Remarks: This new subgenus contains the almost all atypical species of the genus *Asteroteuthis* sensu GRIMPE, 1931. These species are different from *Asteroteuthis* typified by *A. veranyi* in having biserial suckers in the Arms I–III versus tri- or quadriserial suckers.

III. Subgenera of the Genus *Abraliopsis*

The genus *Abraliopsis* was hitherto divided into two subgenera, *Abraliopsis* Joubin, 1896 (s. str.) and *Micrabralia* Pfeffer, 1900. In the present study, two new subgenera are separated from them based on the characters of hectocotylus and tentacle (Table 4).

Table 4. An abridged comparison of selected criteria of four subgenera of the genus *Abraliopsis*.

	Abraliopsis s. s.	*Micrabralia*	*Boreabraliopsis* nov.	*Pfefferiteuthis* nov.
Oral surface of arms	Smooth	Papillated	Smooth	Papillated
Hectocotylization	Subequal flaps	Subequal flaps	Unequal flaps	Subequal flaps
Left Arm IV of male	Normal	Normal	Normal	Modified
Ventral flap of manus	Absent	Present/Absent	Present	Present/Absent
Photophore arrangement on head	Scattered	Linear	Scattered	Linear

1. Subgenus ***Abraliopsis*** JOUBIN, 1896 (s. str.)

Synonym: *Abralia* PFEFFER, 1912 (pars.).

Type species: *Abraliopsis pfefferi* JOUBIN, 1896.

Diagnosis: Photophores on the ventral surface of the head are uniformly scattered. Hectocotylus is composed of two different-sized, offset crests. Protective membrane of the left Arm IV of the male is not modified. Tentacular club has the ventral flap (Figs. 22–23).

Included species:

1. *Abraliopsis hoylei* (PFEFFER, 1884)
2. *Abraliopsis pfefferi* JOUBIN, 1896
3. *Abraliopsis tui* RIDDELL, 1985
4. *Abraliopsis* n. sp. A.

Geographical distribution: Warm waters of the world.

Remarks: Subgenus *Abraliopsis* sensu PFEFFER, 1900, is divisible into two subgenera. This subgenus is characterized by the presence of ventral flap and well-

developed aboral keel of the tentacular club, and the hectocotylus composed of two irregular-sized offset crests.

2. Subgenus *Micrabralia* PFEFFER, 1900

Type species: *Abralia lineata* GOODRICH, 1896.

Diagnosis: Photophores on the ventral surface of the head form distinct longitudinal rows: two continuous crests on the ventral margin and one on the dorsal margin. Hectocotylus in right Arm IV is composed of three subequal-sized offset crests. Protective membranes of the left Arm IV, of which oral surface is smooth, are not modified. The protective membrane of the Arms I–III of the male is somewhat developed than that of the Arm IV and their oral surface is ornamented by many conical papillae.

Included species:

1. *Abraliopsis affinis* (PFEFFER, 1912)
2. *Abraliopsis gilchristi* (ROBSON, 1924).

Geographical distribution: Indian Ocean and South Pacific.

Remarks: This subgenus is characterized by the distinct longitudinal photophore rows on the ventral head, and the presence of ventro-distal crest in the hectocotylus. The papillation on the oral surfaces of the Arms I–III of the male (VOSS, 1967; RIDDELL, 1985) is a remarkable character by which this subgenus is distinguished from the subgenera *Abraliopsis* s.s. and *Boreabraliopsis* nov. The left Arm IV of the male of the present subgenus is not modified to a fleshy web (VOSS, 1967; NESIS, 1982) unlike *Pfefferiteuthis* nov. and lacks conical papillae on its oral surface (VOSS, 1967).

3. Subgenus *Boreabraliopsis* nov.

Synonym: *Watasenia* MCGOWAN & OKUTANI, 1968, non ISHIKAWA, 1913.

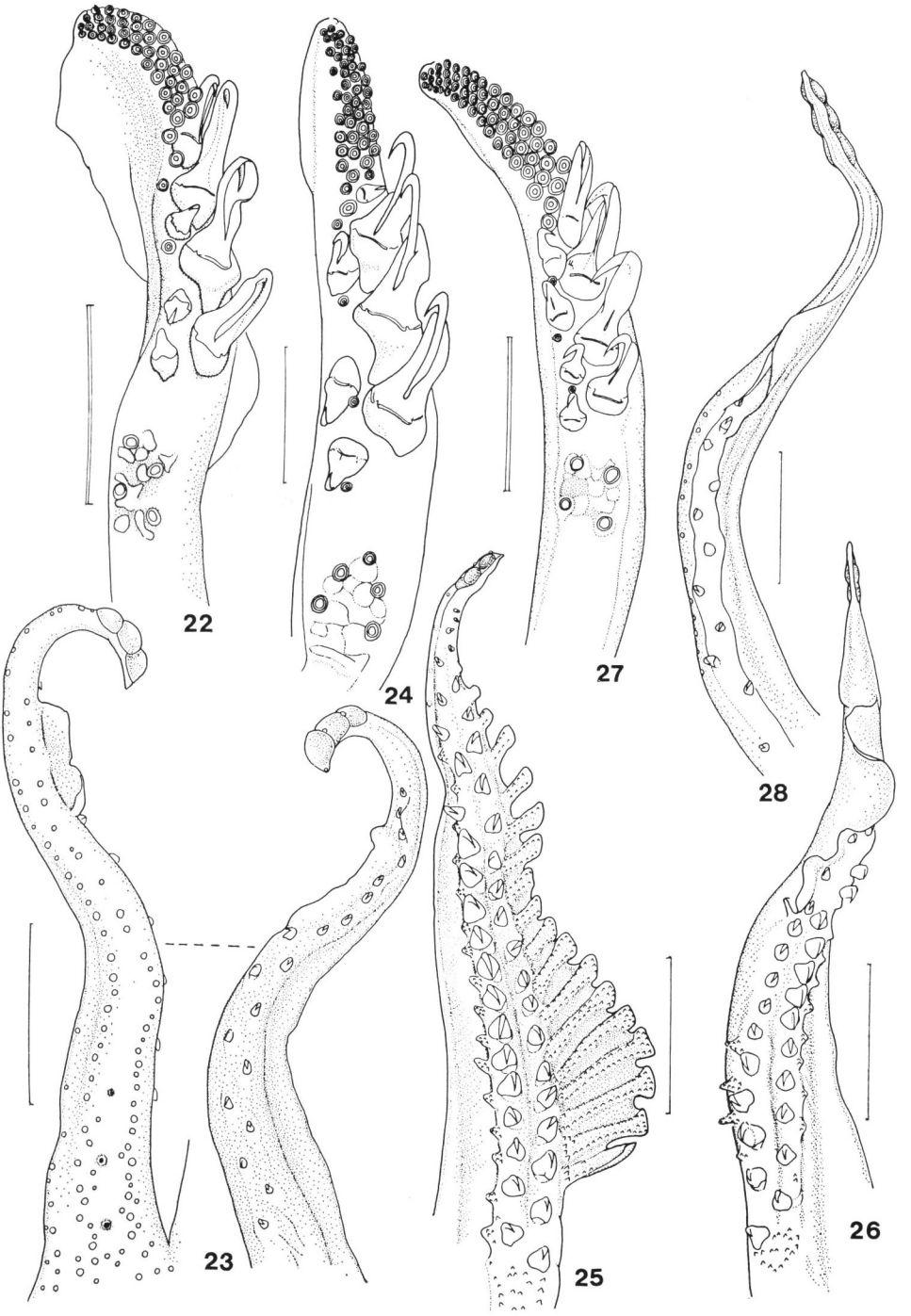
Type species: *Abraliopsis felis* MCGOWAN et OKUTANI, 1968.

Definition: Photophores on the ventral surface of the head is uniformly scattered. Hectocotylus is composed of two subequal-sized offset crests. Protective membrane of the left Arm IV in male is not modified. Tentacular club lacks ventral flap (Figs. 27–28).

Figs. 22–23. *Abraliopsis* (s. s.) sp. A, male (24.9 mm DML) from 36°04.5′N, 157°55.6′E, 150–300 m (*Kaiyo-Maru*, 1972). —— 22. Left tentacle. 23. Hectocotylized arm, oral and lateral views.

Figs. 24–26. *Abraliopsis* (*Pfefferiteuthis* nov.) *falco* YOUNG, 1972, male (32.5 mm DML) from 30°04.2′N, 134°28.0′E, 0–650 m (*Kaiyo-Maru*, 1986). —— 24. Left tentacle. 25. Modified left Arm IV. 26. Hectocotylized arm (right Arm IV).

Figs. 27–28. *Abraliopsis* (*Boreabraliopsis* nov.) n. sp. B. —— 26. Female (33.1 mm DML) from 32°28.8′N, 149°58.2′E, 0–100 m, left tentacle (*Kaiyo-Maru*, 1987). 28. Male (43.3 mm DML) from 37°32.5′N, 147°59.5′E, 0–101 m, hectocotylized arm (*Kaiyo-Maru*, 1987). [Scale bars: 5 mm (simple) or 2 mm (double).]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Included species:

1. *Abraliopsis felis* McGOWAN & OKUTANI, 1968
2. *Abraliopsis* n. sp. B.

Geographical distribution: Warm to cool temperate waters of the Pacific.

Remarks: This new subgenus is characterized by the absence of ventral flap and narrow aboral keel of the tentacular club, and the hectocotylus composed of two subequal-sized offset crests.

4. Subgenus ***Pfefferiteuthis*** nov.

Synonym: *Micrabralia* PFEFFER, 1912 (pars.) nec 1900.

Type species: *Abralia* (*Micrabralia*) *affinis* PFEFFER, 1912.

Diagnosis: Photophores on the ventral surface of the head form distinct longitudinal rows. Hectocotylus in right Arm IV is composed of three subequal sized offset crests: two continuous crests on the ventral margin and one on the dorsal margin. Protective membranes of the left Arm IV are modified into a wide fleshy web, and its oral surface is ornamented by many small conical papillae which are also pronounced on the proximal oral surface of the male's Arms I–III (Figs. 24–26).

Included species:

1. *Abraliopsis affinis* (PFEFFER, 1912)
2. *Abraliopsis falco* YOUNG, 1972
3. *Abraliopsis chuni* NESIS, 1982
4. *Abraliopsis atlantica* NESIS, 1982.

Geographical distribution: Northwest to East Pacific and Atlantic Ocean.

Remarks: The subgenus *Micrabralia* sensu PFEFFER, 1912, is divisible into two subgenera. The present new subgenus is characterized by the distinct longitudinal photophore rows on the ventral head, presence of the ventro-distal crest in the hectocotylus and papillation on the oral surfaces of all arms in male (HOYLE, 1904; CHUN, 1910; YOUNG, 1972). In addition, the modification of the fleshy web of the left Arm IV of the male is a remarkable character that distinguishes the present new subgenus from *Micrabralia* (HOYLE, 1904; CHUN, 1910; YOUNG, 1972; NESIS, 1982).

Conclusive Remarks

The phylogenic relationship of the family Enoploteuthidae have never been discussed until the recent works of ENGESER and CLARKE (1988) and YOUNG and BENNET (1988). Among the genera of this family, *Enoploteuthis* has hitherto been placed at the most primitive position and the genera *Abralia* and *Abraliopsis* in the advanced ones. NESIS (1987) discussed the process of "oceanization" in relation to phylogenetic advancement in order of *Enoploteuthis*, *Enigmoteuthis*, *Abralia*, *Watasenia* and *Abraliopsis*. His scheme matched well with the conventional view. ENGESER and CLARKE (1988) discussed the phylogenic relationship with out-groups such as Onychoteuthidae based on the characters of hooks. They considered that *Abraliopsis* and *Abralia* are more advanced than *Enoploteuthis*. YOUNG and BENNET (1988) placed *Abralia* in the most

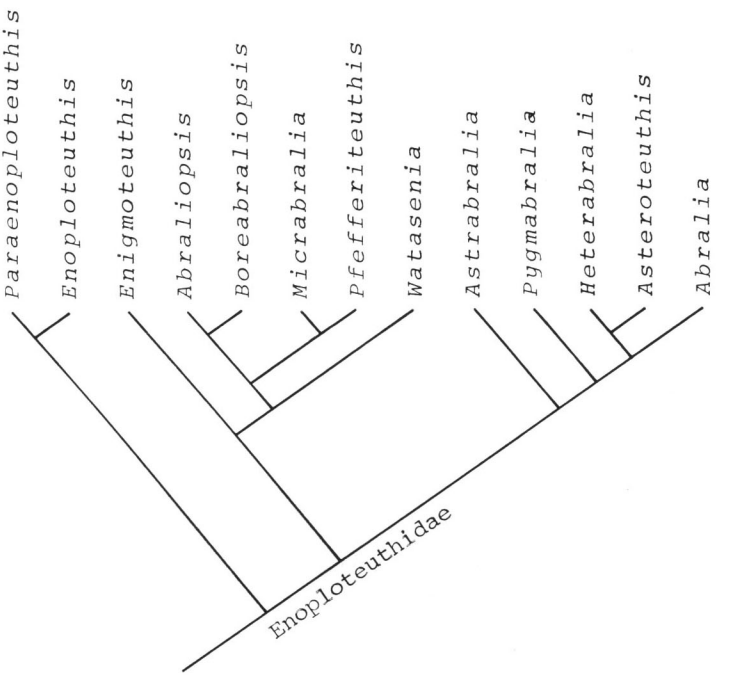

Fig. 29. Possible phylogenetic relationships of genera and subgenera of the Family Enoploteuthidae.

primitive status with *Enoploteuthis* which is derived from the stem of the former, *Abraliopsis* is considered to be the most advanced while *Watasenia* is less advanced than that based on the structure of integumental photophores.

In the present study, 25 characters are subjected to analysis (TSUCHIYA, unpublished), and the result is here tentatively given in form of a dichotomous tree of the genera and subgenera of the Family Enoploteuthidae (Fig. 29).

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