東南アジア赤道域沿岸性甲殻類の生物地理とその成立過程の研究

Crustacean Biogeography in Equatorial area of Southeast Asia

課題番号　１１６９１１７２

平成１１年度～平成１３年度科学研究費補助金
（基盤研究　Ａ２）研究成果報告書

平成１４（２００２）年3月

研究代表者　山口　寿之
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研究目的：

インドおよび西太平洋の甲殻類の生物地理は、テチス海に起源をもち、そして第四紀の氷河性海水準変動による海洋の分断によって多様性を増した。進化（多様性）の中心域であったインド洋と太平洋域の間の東南アジア赤道域における沿岸性甲殻類の多様性の実態を把握し、そこでの生物地理の成立過程や種分化様について考察する。

研究組織

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Prabowo, R.E.（インドネシア：Jenderal Soedirman Univ.・講師）蔓脚類の生物地理
Puspasari, I.A.（インドネシア：Riau Univ.・助教授）蔓脚類の生物地理

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平成１３年度	４，３００	１，２９０	５，５９０
総計	１３，８００	１，２９０	１５，０９０

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山口寿之：東南アジア赤道域の蔓脚類の生物地理

公表論文：

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Puspasari, I.A., T. Yamaguchi, and S. Angsupanich (2000) Reexamination of a Little-known Mangrove Barnacle, *Balanus patelliformis* Bruguière (Cirripedia, Thoracica) from the Indo-West Pacific. *Sessile Organisms,* 16(2):1-13.

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Ross, A. and T. Yamaguchi (2001) Site Selection Wall Development and Biogeography of *Galkinia indica*, an Indo-west Pacific Coral-Inhabiting Barnacle. *Biogeography*, 3:59-68. (Aug. 29, 2001)

Puspasari, I.A., T. Yamaguchi, and A. Ross (2002) New record of *Balanus zhujiangensis* Ren, 1989 (Cirripedia, Balanidae) from Okinawa, Japan. *J. Crustacean Biol.*, 22(2):235-240.

この研究で明らかになった主要な点：

***Balanus patelliformis* Bruguière** の再発見、再記載

Puspasari, I.A., T. Yamaguchi, and S. Angsupanich (2000) 論文にて、*Balanus patelliformis* Bruguière をタイ国（マレー半島両岸）のマングローブから報告した。インド南岸のインド洋に模式地をもつ本種は、Bruguière (1789)の記載以来、報告が無かったので今回の発見は、生物地理的意義が大きいだけでなく、また原記載が 200 年以上前であり、現代的視点で考えた場合、それらの形態の記載は、種を特定できるものでは無かった。

この分類群は *Balanus amphitrite* complex（種群）と形態的類似性が高いことは分かっていた。その種群では、主として殻構造や蔓脚上の装飾などの形態的特徴が分類に重要であるという認識 (Henry & McLaughlin 1976, Yamaguchi 1977) に示されているように、それらの形態的特徴の詳細な観察なくしては、同種群に含まれるか否かまた正しい種の記述が出来ない状況であった。本種の再発見と再記載の意義は、極めて非常に大きい。

内容は、次の論文に報告した。

Puspasari, I.A., T. Yamaguchi, and S. Angsupanich (2000) Reexamination of a Little-known Mangrove Barnacle, *Balanus patelliformis* Bruguière (Cirripedia, Thoracica) from the Indo-West Pacific. *Sessile Organisms,* 16(2):1-13.

また以下に示すように、タイ以外にもベトナムからも発見された。

19990507-1	Changoe canal, Takientong, Surat Thani (Mangrove), Thailand
19990507-2	Tapee River, Surat Thani (River Left side), Thailand
19990507-3	Tapee River, Surat Thani (River mouth, Delta), Thailand
19990507-4	Tapee River, Surat Thani (Zonation) (near mouth, Right side), Thailand

20000727-2	Binh Khanh, Vietnam

新種 *Balanus thailandicus* n. sp. をタイのマングローブから記載報告

Balanus amphitrite 種群に属す新種 *B. thailandicus* n. sp. をタイ南西部のマングローブから記載報告した(Puspasari, Yamaguchi & Angsupanich 2001)。形態は *Balanus amphitrite* 種群に共通の特徴をもつ、そしてその種群の *B. reticulatus*, *B. amphitrite*, *B. patelliformis*, *B. variegatus* と同所性を示す。しかし周殻が成体ではうねった肋を持つが、幼体ではそれを持たず平滑である点、殻構造が他の分類群と異なる点、蔓脚の節数、第三、第四蔓脚に突出したホックを持つなどの違いが、この分類群を新種と判定する理由となる。

内容は、次の論文に報告した。

Puspasari, I.A., T. Yamaguchi, and S. Angsupanich (2001) *Balanus thailandicus* sp. nov., A New Mangrove Barnacle of the *Balanus amphitrite* complex (Cirripedia, Balanomorpha) from Satun, Southwest Thailand. *Sessile Organisms*, 18(1):27-33.

また模式地のタイ南西部 Satun 以外にも、以下に示すように今回の調査でベトナム、インドネシアで新たな生息域を初めて確認した。

19990511-1	Puyu Canal,Tamalung Bay, Satun (Mangrove), Thailand
19990511-2	Tachin Canal, Tamalung Bay, Satun (Mangrove), Thailand
20000306-1	Tachin Canal, Tamalung Bay, Satun (Mangrove), Thailand
20000306-2	Tachin Canal, Tamalung Bay, Satun (Mangrove), Thailand
20000306-3	Tachin Canal, Tamalung Bay, Satun (Mangrove), Thailand
20000307-2	Tanyong Kaboi Canal, Satun (Mangrove), Thailand
20000307-3	Between Tanyong Kaboi & Puyu Canals, Satun (Mangrove), Thailand
20000307-4	Puyu Canal,Tamalung Bay, Satun (Mangrove), Thailand
20000307-6	Puyu Canal,Tamalung Bay, Satun (Mangrove), Thailand
20000727-1	Lam Vien, Vietnam
20000727-2	Binh Khanh, Vietnam
20010902-1	Likupang, Sulawesi, Indonesia
20010910-1	Patotano Port, Sumbawa, Indonesia
20010910-2	Patotano (Mangrove), Sumbawa, Indonesia

Balanus rhizophorae 記載報告

本種は南シナ海、Gulf of Thailand、インド洋に生息が知られていた (Ren & Liu 1979, Ren 1989) 。今回調査でタイ国マレー半島東西岸およびフィリピンでの生息が確認できた。特にフィリピンでの生息は、初確認である。

19990501-1	Hua Khao, Songkhla, Thailand
19990506-1	Tha Sala, north of Nakhon Si Thamarat, Thailand
19990506-2	Pak Nakhon, Phanang Bay (fish capture case), Thailand
19990506-3	Pak Nakhon, Phanang Bay, Thailand
19990506-4	Pak Nakhon, Phanang Bay (Mangrove) , Thailand
19990507-1	Changoe canal, Takientong, Surat Thani (Mangrove) , Thailand
19990507-2	Tapee River, Surat Thani (River Left side) , Thailand
19990510-1	Tak Bai, Narathiwat (open coast) , Thailand
19990511-2	Tachin Canal, Tamalung Bay, Satun (Mangrove), Thailand
20000718-2	Giao Thuy (Mangrove), Thailand
20000728-2	Xa Thang Nhi. Vung Tau, Thailand
20001212-1	Front of Bolinao Marine Institute, Philippines

Balanus zhujiangensis Ren

本種は、中国南部の Zhujiang 川の汽水域から Ren（1989）によって記載報告された種である。Ren (1989) は、この分類群が蓋板表面に見られる特徴から *Balanus trigonus* 種群に含まれると述べ、その類縁関係について記載した。本種は、その後いかなる場所からも発見されたことが無く、Ren (1989) の真偽は明らかにならないまま、ほとんど顧みられなかった。

本種は、原記載の生態とは異なる沖縄のサンゴ礁域から少数個体採集されたフジツボ類の中に類似の形態を持つものが、見つかったことで注目するようになった。サンゴ礁域は近くにかつてマングローブの生育していた河口域を持つ環境であった。形態的類似から比較標本を Ren に依頼し、形態的特徴を Zhujiang 川の汽水域からの Topotype と比較したところ、沖縄標本が *Balanus zhujiangensis* であることが分かった。しかし周殻、口器、第三蔓脚の形態的特徴は、本種が Ren (1989)が考えるように *B. trigonus* との類縁性を考えるよりは、*B. amphitrite* complex との類縁性を考えるのが自然であるという多くの共通する特徴を共有することが明らかになった。この類縁性についてまた日本の沖縄で模式地以外からのはじめての発見となる。

Puspasari, I.A., T. Yamaguchi, and A. Ross (2002) New record of *Balanus zhujiangensis* Ren, 1989 (Cirripedia, Balanidae) from Okinawa, Japan. *Journal of Crustacean Biology*, 22(2)235-240.

Balanus kondakovi Tarasov and Zevina

本種は南西日本、韓国からインド・ボンベイまで知られてきたが、ベトナム、フィリピン、インドネシアでの分布は初めての確認となる。

20000718-1	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000719	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000720-1	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000721-1	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000721-2	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000721-3	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000721-4	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20001212-1	Front of Bolinao Marine Institute, Philippines
20001214-1	Front of Bolinao Marine Institute, Philippines
20010831-2	Bali, Indonesia
20010831-3	Bali, Indonesia

Balanus reticulatus Uitnomi

ほぼ全世界に分布している。

19991002	Motupore Island R C, Papua New Guinea
19991003-1	Motupore I. sd beach, Papua New Guinea
19991003-2	Motupore I. sd beach, Papua New Guinea
19991003-4	Motupore I. ship hull, Papua New Guinea
19991009-1	Jetty, Jais Aben Resort Hotel, Madang, Papua New Guinea
20000718-2	Giao Thuy (Mangrove), Vietnam
20001212-1	Front of Bolinao Marine Institute, Philippines
20001212-2	Aguada, Anda, Philippines
20001212-3	Marimpay, Anda, Philippines
20001212-4	Siepar, Anda, Philippines
20001212-5	Pilar, Santiago Is., , Philippines
20001217-1	Wawa, Batangas City, , Philippines
20010903-1	Batunona, Kauditan, Sulawesi, , Philippines

Balanus variegatus Darwin

本種は、ニュージーランド、オーストラリア、インドネシア、Gulf of Thailand、フィリッピン、台湾、韓国、日本に分布が知られている。今までの情報ではベトナムからは初記録となる。

19990501-1	Hua Khao, Songkhla, Thailand
19990506-1	Tha Sala, north of Nakhon Si Thamarat, Thailand
19990507-3	Tapee River, Surat Thani (River mouth, Delta) , Thailand
19990507-4	Tapee River, Surat Thani (Zonation) (near mouth, Right side) , Thailand
19990510-2	Tak Bai, Narathiwat (Lagoon) , Thailand
19990511-3	Port, Tamalung Bay, Satun, Thailand
20000307-1	Port, Tamalung Bay, Satun, Thailand
20000721-1	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000721-1	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20000726-2	Can Thanh, Can Gio, Vietnam
20000728-4	Mui O Cap, Vung Tau, Vietnam
20001212-4	Siepar, Anda, Philippines
20001216-1	Wawa, Batangas City, Batangas, Philippines
20001217-1	Wawa, Batangas City, Philippines

Balanus venustus Darwin

太平洋からは記録が少ないが、ほぼ世界的に分布する分類群である。

19991009-1	Jetty, Jais Aben Resort Hotel, Madang, Papua New Guinea
20000721-5	Xuan Thuy Ramsar Reserve, Giao Thuy, Vietnam
20010909-3	Bangsal Harbor, Lombok, Indonesia
20010910-1	Patotano Port, Sumbawa, Indonesia

外海に生息するフジツボ類の生物地理

次のような種類が外海に生息する分類群である。*Tetraclita squamosa, Tetraclita japonica, Yamaguchiella coelurescens, Tesseropora rosea, Tetraclitella karandei, Tetraclitella chinensis, Megabalaus* sp., *Capitulum mitella, Ibla cummingi,* Turtle barnacle, *Euraphia intertexta, Chirona amaryllis, Lithotrya nicobarica, Austrobalanus*

今回の研究課題で、採集又は生息が確認できた分類群を地点ごとに以下にまとめた。

Date	Locality	Species name *B.=Balanus, T.=Tetraclita,* *: collection, v: very, f: few, a: abundant
Thailand		
19990501-1	Hua Khao, Songkhla	*B. rhizophorae* (va), *B. variegatus* (f)
19990501-2	Port of Songkhla on pier	*B.* sp.A, *B.* sp.B
19990501-3	South of Songkhla on rock	*Chthamalus* large & small, *B.* sp.
19990502-1	Kata Main Beach S (w. coast of Phuket)	*Chthamalus* sp., *T. squamosa, B. amphitrite* complex (not *B. amphitrite*)
19990502-2	Karon Noi Beach Relax Bay (Merlidian Hotel)	*Chthamalus* sp., *T. squamosa, Tesseropora, Tetraclitella* sp., *B. amphitrite* complex
19990503-1	N. Nakalay Beach of Patong	*Chthamalus* sp., *T. squamosa, Tesseropora, Tetraclitella* sp., *B. amphitrite* complex
19990503-2	N. Nakalay Beach of Patong, Front of Hotel Patong Lodge	*Chthamalus* sp., *T. squamosa, Tesseropora, Tetraclitella* sp.
19990504-1	Cape Panwa (Aquarium)	*Chthamalus* sp., *B. amphitrite, T. squamosa, Ibla cummingi*
19990504-2	Si-Rei Island, Phuket	*Chthamalus* sp., *B. amphitrite*
19990504-3	Nai Yang Beach, Phuket	Turtle barnacles on plastic plate
19990505-1	Kham Island	*Chthamalus* sp., *T. squamosa, Megabalanus* sp. (dead)
19990506-1	Tha Sala, north of Nakhon Si Thamarat	*Chthamalus* sp., *B. rhizophorae, B. amphitrite, B. variegatus*

19990506-2	Pak Nakhon, Phanang Bay (fish capture case)	*B. rhizophorae*, *B. amphitrite*, ???
19990506-3	Pak Nakhon, Phanang Bay	*B. rhizophorae*, *B. amphitrite*, ???
19990506-4	Pak Nakhon, Phanang Bay (Mangrove)	*B. rhizophorae*, *B. amphitrite* (vf). *Chthamalus* sp.
19990507-1	Changoe canal, Takientong, Surat Thani (Mangrove)	*B. patelliformis* (va), *B. rhizophorae* (vf), *B. amphitrite*,
19990507-2	Tapee River, Surat Thani (River Left side)	*B. patelliformis* (va), *Chthamalus* sp. (vf), on 流木 *B. rhizophorae*,
19990507-3	Tapee River, Surat Thani (River mouth, Delta)	*B. variegatus* (va), *B. patelliformis* (vf)
19990507-4	Tapee River, Surat Thani (Zonation) (near mouth, Right side)	*Chthamalus* sp., *B. patelliformis*, *B. variegatus*
19990510-1	Tak Bai, Narathiwat (open coast)	*Chthamalus* sp., *T. squamosa*, *B. rhizophorae*? (潮下帯)
19990510-2	Tak Bai, Narathiwat (Lagoon)	*Chthamalus* sp., *B. variegatus*,
19990511-1	Puyu Canal,Tamalung Bay, Satun (Mangrove)	*B. thailandicus* (type-loc), *B. amphitrite*, (=Loc. 20000307-4)
19990511-2	Tachin Canal, Tamalung Bay, Satun (Mangrove)	*Chthamalus* sp., *B. thailandicus*, *B. amphitrite*, *B. rhizophorae*, (=Loc.20000306-3)
19990511-3	Port, Tamalung Bay, Satun	*Chthamalus* sp., *B. amphitrite*, *B. variegatus*
20000303-1	Padong Beach South, Phuket	*Balanus* spp.*
20000304-1	N. Nakalay Beach of Patong (=990503-1)	*Chthamalus* sp., *T. squamosa*, *Tesseropora**, *Tetraclitella* sp.
20000306-1	Tachin Canal, Tamalung Bay, Satun (Mangrove)	*Chthamalus* sp., *B. thailandicus*, *B. amphitrite*,
20000306-2	Tachin Canal, Tamalung Bay, Satun (Mangrove)	*Chthamalus* sp., *B. thailandicus*, *B. amphitrite*,
20000306-3	Tachin Canal, Tamalung Bay, Satun (Mangrove)	*Chthamalus* sp., *B. thailandicus*, *B. amphitrite*,
20000306-4	Tachin Canal, Tamalung Bay, Satun	*B. amphitrite*
20000306-5	Port, Tamalung Bay, Satun	*B. amphitrite*
20000307-1	Port, Tamalung Bay, Satun	*B. variegatus* (20000306-5 と同じ場所だが1 m以上潮位が下)
20000307-2	Tanyong Kaboi Canal	*B. amphitrite* (va), *Chthamalus* (va), *B. thailandicus* (vf)
20000307-3	Between Tanyong Kaboi & Puyu Canals	*B. amphitrite* (va), *B. thailandicus (vf)*,
20000307-4	Puyu Canal,Tamalung Bay, Satun (Mangrove)	*B. amphitrite* (va), *B. thailandicus* (vf) (=19990511-1, type-loc. of *B. thailandicus)*
20000307-5	Puyu Canal,Tamalung Bay, Satun (Limestone rock)	*Chthamalus*, *B. amphitrite* (va)
20000307-6	Puyu Canal,Tamalung Bay, Satun (Mangrove)	*Chthamalus*, *B. amphitrite* (va), *B. thailandicus* (vf)
20000307-7	Puyu Village, Puyu Canal,	*Chthamalus*, *B. amphitrite* (va),
20000307-8	Yao Island, Tamalung Bay, Satun	*Chthamalus*, *B. amphitrite* (vf),
Papua New Guinea		
19991002	Motupore Island R C	*B. amphitrite**, *B. reticulatus** on hull of SCOMBER
19991002-1	Horse shoe reef	coral barnacle*
19991002-2	Manunouha I.	*E. intertexta**, *T. squamosa*
19991003-1	Motupore I. sd beach	*B. reticulatus**, *B. amphitrite**
19991003-2	Motupore I. sd beach	*Chthamalus* sp.*, *B. reticulatus**, *B. amphitrite**, *T. squamosa**, *Yamaguchiella coelurescens**, *Tesseropora* sp., *Austrobalanus* sp.(dead)
19991003-3	Motupore I. Mangrove	*Chthamalus* sp.*, *T. squamosa*
19991003-4	Motupore I. ship hull	*T. squamosa**, *B. reticulatus**, *Yamaguchiella coelurescens**, *Tesseropora* sp.*
19991003-5	Loloata Is. Jetty	*Balanus* sp.*, *T. squamosa*, *Yamaguchiella coelurescens**, *Tesseropora* sp.*
19991006-1	Alotau (Tagolewa)	*T. squamosa**,*Tesseropora* sp.*, *Yamaguchiella coelurescens**, *Chthamalus* sp.*
19991006-2	Alotau,Tip of peninsula	*T. squamosa**,*Tesseropora* sp.*, *Yamaguchiella coelurescens**, *Chthamalus* sp.*
19991008-1	Nagada Harbour, Jais Aben Resort Hotel, Madang	*Chthamalus* sp.*(Brown)
19991008-2	Island jetty, Jais Aben Resort Hotel, Madang	*Chthamalus* sp.*(Brown), *Chthamalus* sp.*(white), *Euraphia* sp.*, *B. amphitrite**, *Yamaguchiella* sp.*
19991009-1	Jetty, Jais Aben Resort Hotel, Madang	*Chthamalus* sp.*(Brown), *B. amphitrite**, *B. reticulatus**, *B.*

		_venustus_*
19991009-2	Float, Jais Aben Resort Hotel, Madang	_B. amphitrite_*, _Conopea?_ sp.*, _Lepas_ sp.*
Vietnam		
20000717	Xuan Thuy Ramsar Reserve, Giao Thuy	_B. amphitrite_ (dead)
20000718-1	Xuan Thuy Ramsar Reserve, Giao Thuy	（約 200cm) _Chthamalus_ spp.*（丸い平滑と、星型）、(約 150cm レベル） _B. amphitrite_*, _B. kondakovi_*
20000718-2	Giao Thuy (Mangrove)	_B. amphitrite_*, _B. rhizophorae_*, _B. reticulatus_*
20000719	Xuan Thuy Ramsar Reserve, Giao Thuy	_Chthamalus_ spp.*, _B. amphitrite_*, _B. kondakovi_*
20000720-1	Xuan Thuy Ramsar Reserve, Giao Thuy	_Chthamalus_ spp.*, _B. amphitrite_*, _B. kondakovi_*
20000721-1	Xuan Thuy Ramsar Reserve, Giao Thuy	水路のコンクリート:上から _Chthamalus_ sp.*, _B. amphitrite_*, _B. kondakovi_*, _B. variegatus_*
20000721-2	Xuan Thuy Ramsar Reserve, Giao Thuy	Saltmarsh of mud bottom; _Chthamalus sp._*, _B. kondakovi_*, _B. thailandicus_, _B. kondakovi_, _B. amphitrite_
20000721-3	Xuan Thuy Ramsar Reserve, Giao Thuy	muddy sand beach of river mouth; _Chthamalus_ sp.*, _B. kondakovi_*
20000721-4	Xuan Thuy Ramsar Reserve, Giao Thuy	muddy sand beach of river mouth; _Chthamalus_ sp*., _B. kondakovi_*
20000721-5	Xuan Thuy Ramsar Reserve, Giao Thuy	Drift wood on the muddy sand bottom; _B. venustus_*
20000725-1	Foresty Park, Can Gio	マングローブの Canal（水路）; _B. thailandicus_*, _Chthamalus_ sp.*
20000725-2	Can Thanh, Can Gio	木についたフジツボ; _B. amphitrite_*, _B. variegatus_*
20000726-1	Can Thanh, Can Gio	Can Thanh の市場; 泥干潟; _B. amphitrite_*, _B. variegatus_*, _Chthamalus_ sp.* 泥干潟に横たわっていた丸太の木に _B. variegatus_*, _T. japonica_*(大きい、1年以上の年齢を持つもので、2個体発見).
20000726-2	Can Thanh, Can Gio	Sand Beach; _B. amphitrite_*, _B. variegatus_*, _B. venustus_*
20000726-3	Can Thanh, Can Gio	積み石堤の頂上（海面から 2.5m 以上うえ）; _T. japonica_*, _T. squamosa_*, _Tetraclita_ sp.*
20000727-1	Lam Vien	Museum の先の橋の下；B. _thailandicus_*
20000727-2	Binh Khanh	フェリーターミナル；_B. patelliformis_*, _B. thailandicus_*
20000728-1	Vung Tau	Chau Thanh(20000728-1)港では _B. amphitrite_*
20000728-2	Xa Thang Nhi. Vung Tau	レキ浜のレキ;_T. japonica?_*、 _B. amphitrite_*, _B. rhizophorae_*
20000728-3	Mui O Cap, Vung Tau	Rocky shore; _Chthamalus_*, _T. squamosa_*, _Capitulum mitella_*, _Tetraclitella_ sp.*
20000728-4	Mui O Cap, Vung Tau	_Chirona amaryllis_*(潮下帯も), _T. squamosa_*, _B. variegatus_*
Philippines		
20001212-1	Front of Bolinao Marine Institute	_B. amphitrite_*, _B. reticulatus_*, _B. kondakovi_*, _B. rhizophorae_*, _Chthamalus_
20001212-2	Aguada, Anda	_B. reticulatus_*
20001212-3	Marimpay, Anda	_B. amphitrite_, _B. reticulatus_
20001212-4	Siepar, Anda	_B. amphitrite_*, _B. variegatus_*
20001212-5	Pilar, Santiago Is.	_B. amphitrite_*, _B. reticulatus_*
20001213-1	Silaque Island	_Chthamalus_
20001214-1	Front of Bolinao Marine Institute	_B. amphitrite_*, _B. kondakovi_*, _T. chinensis_*, _Chthamalus_ *
20001214-2	Patar (Light house)	_Chthamalus_, dead _Megabalanus_
20001214-3	Lucap (Lucup でない)	_Chthamalus_
20001216-1	Wawa, Batangas City, Batangas	_B. amphitrite_*, _B. variegatus_*, _B._ sp.* (unlike _B. kondakovi_)
20001216-2	Vistamar Resort Beach, Anilao, Batangas	_Capitulum mitella_, _Ibla_, _Yamaguchiella_, _Chthamalus_
20001216-3	San Teodoro near Cazador Pt., Batangus	_Capitulum mitella_, _Ibla_, _Yamaguchiella_, _T. squamosa_, _Chthamalus_
20001217-1	Wawa, Batangas City	_B. amphitrite_*, _B. reticulatus_*, _B. variegatus_*
20001218-1	Shangri-La's Mactan Island Resort, Mactan Island	_T. squamosa_*, _T. japonica?_*, _T. divisa_*, _T. karandei?_*, _Capitulum mitella_*, _Ibla_*, _Chthamalus_*
20001219-1	Monument, Mactan Island	_Chthamalus_ spp.
20001219-2	Shangri-La's Mactan Island Resort, Mactan Island	_Tesseropora_, _T. squamosa_, _T. japonica?_, _T. divisa_, _T. karandai?_, _Yamaguchiella coerulescens_, _Chthamalus_ spp., _Ibla_,
Indonesia		
20010827	Serangan Island, Bali	_Chthamalus_*, _B. amphitrite complex_*, by Tanaka-san
20010829-1	Soka, Bali	_Chthamalus_*
20010829-2	Gilimanuk, Bali	_Chthamalus_*, _Capitulum mitella_*, _Ibla cumingi_* (150cm), _Chthamalus_*, _Yamaguchiella coerulescens_* (+30cm),
20010829-3	Labuhan Lalang, Bali	_Chthamalus_*, _Chthamalus_*, _Chthamalus_*, _Tesseropora rosea_*,

		_Yamaguchiella coerulescens_*
20010830-1	Yehsarih-1, Bali	_Chthamalus_*, _Yamaguchiella coerulescens_*, _T. squamosa_* (3 ind.),
20010830-2	Yehsarih-2, Bali	_Chthamalus_*, _Yamaguchiella coerulescens_*, _Tesseropora_*, _Tetraclita squamosa_*, _Tetraclitella chinensis_*
20010830-3	Singaraja Harbor, Bali	_Chthamalus, Yamaguchiella coerulescens, Megabalanus?_*
20010831-1	Nusa Dua, Bali	_Chthamalus, Yamaguchiella coerulescens_*, _Tesseropora_*, _Megabalanus_*, _Capitulum mitella_*, _Lithotrya nicobarica_*
20010831-2	Bali	_Chthamalus_*, _Balanus amphitrite_*, _B. amphitrite_ complex*, _B. kondakovi?_*
20010831-3	Bali	_Chthamalus, B. amphitrite_*, _B. amphitrite complex_*, _B. kondakovi?_*
20010902-1	Likupang, Sulawesi	_Chthamalus, T. squamosa, B. thailandicus?_*, _B. amphitrite_ complex*
20010902-2	Munte, Likupang, Sulawesi	_B. amphitrite_ complex*
20010903-1	Batunona, Kauditan, Sulawesi	_Chthamalus_*, _Tetraclitella_*, _Tesseropora rosea_*, _B. amphitrite_*, _B. reticulatus_*, *
20010903-2	Bak, Bitung, Sulawesi	_Chthamalus_*, _Tesseropora rosea_*, _T. squamosa_*, _Yamaguchiella coerulescens_*, _Capitulum mitella_*, _Ibla cumingi_*, _B. amphitrite_ complex*
20010903-3	Tasik Ria Hotel, Manado	_Chthamalus_*, _T. squamosa_*, _Capitulum mitella_*
20010904-1	Batukapal	_Chthamalus_*, _T. squamosa_*, _Capitulum mitella_*, _Lithotrya nicobarica_*, _Tesseropora rosea_*, _Yamaguchiella coerulescens_*, _Tetraclitella chinensis_*, _Tetraclitella karandai_*
20010904-2	Tasik Ria Hotel, Manado	_Chthamalus_*, _T. squamosa_*, _Capitulum mitella_*, _Tesseropora rosea_*, _Yamaguchiella coerulescens_*, _Tetraclitella chinensis_*, _Tetraclitella karandai_*, _Ibla cumingi_*, _B. amphitrite_ complex*
20010906-1	Kristal Hotel Front, Kupang	_Lepas_*
20010907-1	Tobloong, Kupang	_Yamaguchiella coerulescens_*, _Tesseropora_*, _T. squamosa_*, _Chthamalus_ (Large)*, _Yamaguchiella coerulescens_ (Juvenile)*, _Lithotrya nicobarica_*, _Chthamalus_ (S)*
20010907-2	Barate North Beach	_T. squamosa_*, _Chthamalus_ (L)*, _Chthamalus_ (S)*, _Euraphia intertexta_*, _Yamaguchiella coerulescens_*, _Capitulum mitella_*, _Lithotrya_*
20010908-1	Tenau Port, Kupang	_T. squamosa_*,_Yamaguchiella coerulescens_*, _Chthamalus_ (L)*, _Chthamalus_ (S)*, _Tesseropora rosea_ + green*, _B. amphitrite_ complex*, _Tetraclitella chinensis_*
20010909-1	Lembar Port, Lombok	_B. amphitrite_*
20010909-2	Senggigi, Lombok	_Chthamalus_*, _T. squamosa_ + sp.?*, _Yamaguchiella coerulescens_*, _Capitulum mitella_*
20010909-3	Bangsal Harbor, Lombok	_Chthamalus_*, _T. squamosa_ *, _Yamaguchiella coerulescens_*, _Capitulum mitella_*, _Tesseropora rosea_*, _Ibla cumingi_*, _Tetraclitella chinensis_*, _B. venustus_*
20010910-1	Patotano Port, Sumbawa	_Chthamalus_*, _T. squamosa_ *, _Yamaguchiella_*, _Tesseropora rosea_*, _Tetraclitella chinensis_*, _B. venustus_*, _B. thailandicus_?:,
20010910-2	Patotano (Mangrove), Sumbawa	_Chthamalus_*, _Tetraclitella_*, _B. thailandicus_?*
20010910-3	South of Taliwang, Sumbawa	_Chthamalus, T. squamosa, Capitulum mitella, Yamaguchiella,_

*: collection, v: very, f: few, a: abundant

向井　宏：海草およびモエビ類に関する報告

熱帯性海草は、太平洋およびインド洋に約２０種が知られており、もっともその多様性が高いのが、インドネシア・パプアニューギニア・マレー半島に囲まれた海域である。そこを中心として、海草の種多様度は主要な海流（黒潮、東オーストラリア海流、反赤道海流）に沿って分布し、分布の中心から遠くなるにつれて多様度が減少し、ハワイ、マーシャル群島、タヒチなどでは 1 種もしくは 0 種になっている。

海草の葉上に生活の場を得ているモエビ類については、今までほとんどその分布に関するデータが調べられていなかった。分類群としてモエビ類に含まれるエビの報告はそれぞれの地域から多少は知られているが、それは海草の葉上から採集されたかどうかについては、今までの報告はまったく触れられておらず、真に葉上性のモエビであるかどうかは疑問が大きい。今回、はじめて海草葉上からの採集されたモエビ類に限った調査が行われた。その結果、いまだ多くの個体について同定の途中にあるが、熱帯海草藻場におけるモエビ類の種がかなり共通なものが多いことが明らかになりつつある。ただし、最終的な同定によっては、もう少し地域ごとの種の違いが多くなる可能性は残っている。どちらにしても、西太平洋の海草藻場に広く分布する種が多いが、種によっては、一つの藻場からしか採集されなかったものもあり、分布範囲は種によって異なるということができる。その分布の範囲は海草の多様度の分布と必ずしも一致していない。海草の分散が、比較的どの種においても似た分散様式をもつのに対して、モエビ類の分散様式は、種によって異なること、とくに、流れ藻となった海草による「いかだ効果」による分散が、モエビ類の分布を考える key idea になると考えられる。

採集地点での採集品のリストおよび生物地理に関する考察

採集地点および出現種リスト

★パプア・ニューギニア　Motupore island (Bootles Bay)
海草
1.*Halodule uninervis*
2.*Cymodocea rotundata*
3.*C. serrulata*
4.*Syringodium isoetifolium*
5.*Enhalus acoroides*
6.*Thalassia hemprichii*
7.*Halophila ovalis*
モエビ類
1.*Periclimenes indicus* (Kemp)
2.*Periclimenes* sp.
3.*Hippolyte ventricosa*
4.*Hippolyte* sp.
5.*Latreutes pygmaeus* Nobili
6.*L. porcinus* Kemp
7.*Chlorocurtis jactans* (Nobili)
8.*Heteropaeneus longimanus* de Man
9.*Scyonella maldivensis* Borradaile

★パプア・ニューギニア　Milne Bay
★パプア・ニューギニア　Madan
海草
1.*Enhalus acoroides*
2.*Thalassia hemprichii*
3.*Halophila ovalis*
モエビ類
未同定

★タイ　Ko Si Chang
海草・モエビ類
なし

★タイ　Phuket
海草
1.*Cymodocea rotundata*
2.*Thalassia hemprichii*
3.*Halophila ovalis*
モエビ類
1.*Periclimenes indicus* (Kemp)
2.*Periclimenes* seischellensis
3.*Hippolyte ventricosa*
4.*Hippolyte* sp.
5.*Latreutes porcinus* Kemp
6.その他、未同定数種

★タイ　Haad Chao Mai (Trang)
海草
1.*Halodule uninervis*
2.*Cymodocea rotundata*
3.*C. serrulata*
4.*Syringodium isoetifolium*
5.*Enhalus acoroides*
6.*Thalassia hemprichii*
7.*Halophila ovalis*
モエビ類
1.*Periclimenes indicus* (Kemp)
2.*Hippolyte ventricosa*
3.*Hippolyte* sp.
4.*Latreutes pygmaeus* Nobili
5.*L.* sp.
6.その他、未同定数種

★ベトナム　Dam Lang Co (Thua Thien Hue),
海草
1.*Zostera japonica*

2.Halodule pinifolia
3.Thalassia hemprichii
4.*Halophila ovalis*
モエビ類
未同定

★ベトナム　Dam Giang-Cau Hai Lagoon (Hue),
海草
1.Halodule pinifolia
2.Zostera japonica
3.*Halophila ovalis*
4.*Ruppia martima*?
モエビ類
未同定

★フィリピン　Puerto Galera (Mindoro island)
海草
1.Cymodocea serrulata
2.Syringodium isoetifolium
3.Enhalus acoroides
4.Thalassia hemprichii
5.*Halophila ovalis*
モエビ類
未同定

★フィリピン　Pandan Island (Honda Bay, Palawan), Puerto Princessa
海草
1.Halodule uninervis
2.H. pinifolia
3.Cymodocea rotundata
4.C. serrulata
5.Syringodium isoetifolium
6.Enhalus acoroides
7.Thalassia hemprichii
8.*Halophila ovalis*
モエビ類
未同定

★フィリピン　Mactan island (Cebu)
モエビ類
1.*Processa australiensis* Baker
2.*Processa* sp. (aff. *hawaiensis*)
3.*Nikoides danae* Paulson
4.*Peliclimenes seychellensis* Borradaile
5.*Alpheus* sp.

論文：
Mukai, H. (1993) Biogeography of the tropical seagrasses in the Western Pacific. *Aust. J. Mar. Freshw. Res.*, 44:1-17

英文要旨

Highest diversity of tropical seagrass species in the Western Pacific has been known in Indonesia, Malaysia, and Papua New Guinea. Along the main ocean currents, the diversity reduced to 0 or 1 species in Hawaii, Marshall islands, and Tahiti. Grass shrimps living on seagrass leaf have been unknown in geography and biodiversity, because past records did not distinguish between shrimps on seagrasses and other habitats. The present survey is the first study on geography of grass shrimps only living on seagrass leaf. Although many specimens are processing to identify, it is appeared that most species of grass shrimps in Papua New Guinea, Thailand, Viet Nam, and Philippines, are common. However, some species are restricted to one or narrow geographical area, so far as I can identify in current knowledges. In conclusion, the geographical range of grass shrimps on seagrass leaf is common in most species, follows to that of seagrasses, but it would be different in different with species. The pattern of ranges in grass shrimps is not always consist to that of seagrass species. In contrast to similar dispersion pattern in seagrasses, the dispersion pattern in grass shrimps varied markedly with species. In particular, 'raft effects' by drifting seagrass shoots on grass shrimps' dispersion would be key idea in consideration of geographical distribution in grass shrimps on seagrass leaf.

和田恵次：十脚カニ類の行動生態と生物地理

Species of the family Ocypodidae (Crustacea, Brachyura) collected in Vietnam, Philippines and Indonesia by the survey in 2000 and 2001, are listed as below. Total number of species is 23 in Vietnam, 15 in Philippines and 14 in Indonesia. Among them, newly recorded species are: *Ocypode ceratophthalma*, *O. stimpsoni*, *Scopimera bitympana*, *Ilyoplax lingulata*, *I. orientalis*, *I. punctata*, *Macrophthalmus convexus*, *M. laevimanus*, *M. sulcatus*, *M. definitus*, and *M. etato* for Vietnam, *Scopimera globosa*, *Ilyoplax* aff. *orientalis*, *Tmethypocoelis choreutes*, *Macrophthalmus crinitus* and *M. holthuisi* for Philippines, and *Ilyoplax integra*, *I.* aff. *orientalis* and *Tmethypocoelis* sp. for Indonesia.

Two undescribed species have been found from Philippines and Indonesia: *Ilyoplax* aff. *orientalis* from the both countries and *Tmethypocoelis* sp. from Indonesia. *Ilyoplax* aff. *orientalis* is morphologically similar to I. *orientalis* and *I. tansuiensis*, but the pattern of waving display by the undescribed species is distinct from the two species that show the same waving pattern. Molecular phylogenetic analysis has revealed that *I. orientalis* and *I. tansuiensis* are more related to each other than to *I.* aff. *orientalis*. Another undescribed species from Bali, Indonesia, *Tmethypocoelis* sp. shows distinctive feature of male pleopod from other congeneric species, but exhibits the same pattern of waving display as that of *T. choreutes*.

Comparison of species composition among the three regions (Vietnam, Philippines and Indonesia) by Jaccard′s coefficient of community, has revealed that Philippines and Indonesia are more similar to each other than to Vietnam (Philippines vs Indonesia: 0.45, Philippines vs Vietnam: 0.12, Indonesia vs Vietnam: 0.19). This finding implies that ocypodid crab fauna of Philippines and Indonesia have a closer affinity to each other than to Vietnam.

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Records of ocypodid crabs from Vietnam, Philippines, and Indonesia

Wada, Keiji

Species	Vietnam		Philippines		Indonesia	
	North	South	Luzon	Mindoro	Bali	Sulawesi
Subfamily Ocypodinae						
Genus *Ocypode*						
O. ceratophthalma	+		+			+
O. stimpsoni		+				
Genus *Uca*						
U. acuta	+					
U. annulipes					+	+
U. borealis	+					

U. dussumieri		+			+	+
U. lactea	+					
U. perplexa		+	+		+	+
U. triangularis			+		+	
U. typhoni			+			
U. vocans			+	+	+	+
Subfamily Dotillinae						
Genus *Scopimera*						
S. bitympana	+					
S. globosa				+		
Genus *Ilyoplax*						
I. formosensis	+					
I. integra					+	+
I. lingulata		+				
I. ningpoensis	+					
I. orientalis		+				
I. aff. *orientalis*			+			+
I. punctata		+				
I. serrata	+	+				
Genus *Tmethypocoelis*						
T. ceratophora	+					
T. choreutes			+			
T. sp					+	
Genus *Dotilla*						
D. wichmanni	+	+			+	
Subfamily Macrophthalminae Genus *Macrophthalmus* Subgenus *Macrophthalmus*						
M. abbreviatus	+					
M. convexus		+	+	+		+
M. laevimanus		+				
M. molloti			+	+		
M. sulcatus		+				
Subgenus *Mareotis*						
M. crinitus				+		+
M. definitus	+		+	+	+	+
M. pacificus	+					
M. tomentosus	+	+				
Subgenus *Paramareotis*						
M. erato	+	+				
M. holthuisi			+	+		
Subgenus *Mopsocarcinus*						
M. bosci			+			

Molecular phylogeny of grapsoid and ocypodoid crabs with special reference to the genera *Metaplax* and *Macrophthalmus*

Kitaura, J., K. Wada, and M. Nishida

Some species of the genus *Metaplax* belonging to the family Grapsidae have occasionally been reported to perform waving display that is a characteristic behavior in the family Ocypodidae but uncommon in grapsids. The morphology and life styles of species of *Metaplax* are also quite similar to those of the genus *Macrophthalmus* of ocypodids. To examine whether ecological and morphological similarities between *Metaplax* and *Macrophthalmus* are based on convergent evolution or their common evolutionary history, 846-bp nucleotide sequences from the 16S mitochondrail ribosomal RNA gene of 19 grapsids, 10 ocypodids, and 3 camptandriids, including four species of *Metaplax* (*M. elegans*, *M. takahashii*, *M. shenii* and *M. distincta* from Vietnam) and four species of *Macrophthalmus*, (*M. latreillei* from Australia, and *M. banzai*, *M. brevis* and *M. quadratus* from Japan) were analyzed. The resultant phylogenetic tree revealed that both families Grapsidae and Ocypodidae are polyphyletic. *Macrophthalmus* was distinct from any other ocypodid genera studied, forming a sister group relationship with grapsid species of the subfamily Varuninae, and *Metaplax*, *Cyclograpsus* and *Helice* of the subfamily Sesarminae. *Metaplax*, *Cyclograpsus* and *Helice* were found to be more closely related to Varuninae than to other Sesarminae species, indicating that the subfamily Sesarminae is polyphyletic. These relationships were in agreement with the distribution pattern of a tRNAVal gene rearrangement on the inferred tree. This molecular phylogenetic analysis suggests that the behavioral and morphological similarities observed between *Metaplax* and *Macrophthalmus* are probably due to convergent evolution, despite a close phylogenetic relationship. The waving display in intertidal crabs of the families Grapsidae and Ocypodidae may have evolve several times in their lineages, associated with exposed semi-terrestrial habitat of the intertidal environment.

The evolution of social behaviors in sentinel crabs (Brachyura: Ocypodidae: *Macrophthalmus*): implications from molecular phylogeny

Kitaura, J., M. Nishida, and K. Wada

Crabs of the genus *Macrophthalmus* have been known to exhibit highly developed and diverse social behaviors, such as allocleaning, fighting and waving display behaviors. To understand the evolutionary pathway of these social behaviors, 978-pb nucleotide sequences from mitochondrial 16S rRNA genes of 19 species of *Macrophthalmus* (11 species from Japan, 6 species from Australia and 2 species from Vietnam), with 2 grapsid species as outgroup taxa, were analyzed and reconstructed a molecular phylogeny. The resultant tree showed that *M. latifroms* (subgenus *Tasmanoplax*) was branched first, followed by *M. boteltobagoe* (subgenus *Paramareotis*) and the other species were the branched successively, and that the subgenus *Macrophthalmus* and *Paramareotis* were polyphyletic, with two separate lineage, respectively, indicating inconsistencies with the relationship inferred from their morphological features. The species having similar habitat conditions showed similar morphological features though they are not phylogenetically close relative.

Allocleaning behavior was widely observed throughout the genus *Macrophthalmus*, and phylogenetic analysis of this behavior suggests that it has evolved once in their early history of the lineage. Fighting behavior between males could be classified into grasping fight (*M. milloti*, *M. banzai*, *M. definitus*, *M. japonicus*, *M. bosci*) and arm-extending fight (*M. abbreviatus*, *M. brevis*, *M. convesus M. latifrons*, *M. boteltobagoe*). Arm-extending fight was more complex behavior in comparison with grasping fight, and the analysis demonstrated that species with arm-extending fight are found in the most ancestral part of the phylogeny. The analysis also revealed that arm-extending fight has evolved secondarily two times in their lineage, suggesting fighting behavior does not bear enough phylogenetic components. Waving display behavior observed in *Macrophthalmus* can be roughly divided into 4 patterns, non-forward vertical type (*M. convexsus*, *M. milloti*, *M. darwinensis*, *M. definitus*, *M. japonicus*, *M. pacificus*, *M. tomentosus*), forward vertical type (*M. brevis*, *M. bosci*), non-forward lateral type (*M. banzai*) and forward lateral type (*M. erato*, *M. quadratus*). The superimposition of these four types indicates that non-forward lateral type has evolved from non-forward vertical type, and forward lateral type has evolved from forward vertical type. This scenario also appeared reasonable with respect to the behavioral trends of their cheliped movement in waving display.

田中次郎：藻類の系統分類と生物地理分類学ー

田中次郎（東京水産大学資源育成学科）

東南アジア（タイ・ベトナム・フィリピン・インドネシア）におけるマングローブ汽水域の多細胞藻類の分布と形態

小堀陽子・田中次郎（東京水産大学）
「ベトナム産ササバアヤギヌCaloglossa leprieuriiの生殖体の形態」日本藻類学会２５回大会（2001 東京）

注目すべき分類群

１．インドネシア産ホソアヤギヌ*C. ogasawaraensis*

インドネシア，Serangan Is.で採集された標本は，節間部が細長く，同一平面上で外生枝によってのみ分枝を行う事から*C. ogasawaraensis*と同定された。他の地域に生育する同種個体群に比べて小型であり，節部付近で多数の枝が生じる。節間部は時折，翼細胞を欠き柄のような形態をみせる。成熟した雌雄の配偶体と四分胞子体を含んでいた。

温帯に生育する*C. ogasawaraensis*の季節消長については，吉崎ら (1986)による千葉県木戸川での調査や，田中・村上(1996)による東京湾の河川，樫村(1998)の茨城県木戸川での調査などによって，成熟した配偶体の存在比が極めて低いと報告されている事から，雌雄の配偶体を含むSerangan Is.産の標本は*C. ogasawaraensis*においては特殊な例だと考えられる。

２．アヤギヌ複合分類群（*C. monosticha*, *C. postiae*, *C.* sp.）

*C. continua*と*C. monosticha*, *C. postiae*は共に内生枝をもち，側軸の第一中軸細胞の内側に周心細胞がある。この形質をもつ分類群は，King and Puttock (1994)において全て*C. continua*に分類され，４亜種が記載されていた。その後，節部の中軸細胞が主軸側に形成する細胞列数と藻体の幅から，多列／幅広型は*C. continua*, 単列／幅広型は*C. monosticha*, 多列／幅狭型は*C. postiae*として新たに種の階級で記載された(Kamiya *et al.* 1997, 1999)。

Kamiya *et al.* (1997, 1999)に従い，Nakhon Si Thammarat（タイ）とGiao Thuy（ベトナム），Benoa Bay（インドネシア）で採集された標本の節間部の長さと幅，節部中軸細胞から生じる細胞列数を測定した。また，Benoa Bay（インドネシア）の試料には，極端に幅の広い個体と狭い個体が混生していたので，それらはそれぞれ別の個体群として扱った。

その結果，Nakhon Si Thammarat（タイ）とBenoa Bay（インドネシア）の幅の狭い個体群は多列／幅狭型で*C. postiae*, Benoa Bay（インドネシア）の幅の広い個体群は単列／幅広型で*C. monosticha*であると考えられた。しかしGiao Thuy（ベトナム）の標本は，節間部の長さと幅では*C. postiae*と*C. monosticha*の中間に位置し，細胞列数は77%が２，３列で多列であった。この結果は温帯に生育する*C. continua*に似ているが，*C. continua*とは細胞列数のほとんど４列以上である点で異なる。そのため，Giao Thuy（ベトナム）産の標本は同定が困難であり，*Caloglossa* sp.として記録した。

フィリピン・インドネシアの出現種

	Philippines			Indonesia				
	1	2	3	4	5	6	7	8
Catenella nipae			+	+	+		+	
C. impudica				+				
C. sp.							+	
Bostrychia tenella						+		
B. binderi			+				+	
B. radicans	+				+		+	
Stictosiphonia kelanensis	+	+			+		+	
Caloglossa adhaerens	+	+		+	+		+	
C. ogasawaraensis	+			+	+		+	

C. leprieurii	+			+	+		+	
C. monosticha				+	+		+	
C. postiae	+		+	+	+		+	

1. Bolinao, Luzon Isl., Philippines, 2. Wawa River, Batangas, Luzon Isl., Philippines, 3. Mactan Isl., Cebu Isl., Philippines, 4. Benoa Bay, Bali, Indonesia, 5. Serangan Isl., Benoa Bay, Bali, Indonesia, 6. Jimbaran, Bali, Indonesia, 7. Gilimanuk, Bali, Indonesia, 8. Labuhan Lalang, Bali, Indonesia

注目すべき分類群

１．ベトナム産*Caloglossa leprieurii*（ササバアヤギヌ）

ベトナムのホーチミン市から南方50km、Can Gioのマングローブ林内で採集された標本は、内生枝をもち、側軸の第一中軸細胞の内側に周心細胞がないことから*C. leprieurii*と同定された。標本は体長1.0-3.2mm、節間部の最大幅の平均は128μmと大変に小型で、節部から一枚葉の内生枝を多数生じる。成熟した雌雄の配偶体と四分胞子体を含んでおり、それぞれ枝の先端付近に生殖器官を形成していた。

Kamiya *et al.*（1995, 1998）では、*C. leprieurii*の形態を細胞列数と藻体幅の二つの形質により区別している。(1)細胞列数：アヤギヌ属は藻体の中央に中軸細胞を持ち、節部において主軸と側軸に分枝する。分枝後、主軸の第一中軸細胞が外側に向けて生じる細胞列数を1列しか持たない単列のグループと２～５列持つ多列のグループがある。(2)藻体幅：単列グループの藻体幅は比較的一定して広いが、多列のグループの藻体幅は広い個体と極端に細い個体がみられる。これら二つの形質を組み合わせ、「単列／幅広型」、「多列／幅広型」、「多列／幅狭型」の３つの形態が報告されている。

Can Gio産*C. leprieurii*の標本がどの形態に含まれるのか明らかにするために、細胞列数と藻体幅を測定し、Kamiya *et al.*（1995）と比較した。その結果、細胞列数は単列、藻体幅は0.07-0.2mmと幅の狭い方に位置し、３つの形態のいずれにも含まれない単列／幅狭型であると考えられた。

２つの形質は、培養条件によっては一部が多列型になった、また、幅広型の藻体幅が0.2-1.2mmまで変動した（Kamiya *et al.* 1995）とある。そのため、Can Gio産の標本は報告されている３つの形態いずれかの生長途中のものではないかと推測した。

２．ベトナム産*C. beccarii*

ベトナム、Can Gioで採集された試料にだけ見られた。*C. beccarii*は内生枝をもたず、節部付近の翼細胞から不定枝を形成する。そのため節部から3本以上の枝が出るように見える。藻体は節部でくびれる。これらの形質は*C. ogasawaraensis*および*C. stipitata*と共通するが、節間部の長さと幅、主枝から側枝の出る角度などが異なる。

３．インドネシア産ホソアヤギヌ*C. ogasawaraensis*

インドネシア、Serangan Is.で採集された標本は、節間部が細長く、同一平面上で外生枝によってのみ分枝を行う事から*C. ogasawaraensis*と同定された。他の地域に生育する同種個体群に比べて小型であり、節部付近で多数の枝が生じる。節間部は時折、翼細胞を欠き柄のような形態をみせる。成熟した雌雄の配偶体と四分胞子体を含んでいた。

温帯に生育する*C. ogasawaraensis*の季節消長については、吉崎ら(1986)による千葉県木戸川での調査や、田中・村上(1996)による東京湾の河川、樫村(1998)の茨城県木戸川での調査などによって、成熟した配偶体の存在比が極めて低いと報告されている事から、雌雄の配偶体を含むSerangan Is.産の標本は*C. ogasawaraensis*においては特殊な例だと考えられる。

４．アヤギヌ複合分類群（*C. monosticha*, *C. postiae*, *C.* sp.）

*C. continua*と*C. monosticha*、*C. postiae*は共に、内生枝をもち、側軸の第一中軸細胞の内側に周心細胞がある。この形質をもつ分類群は、King and Puttock (1994) において全て*C. continua*に分類され、４亜種が記載されていた。その後、節部の中軸細胞が主軸側に形成する細胞列数と藻体の幅から、多列／幅広型は*C. continua*、単列／幅広型は*C. monosticha*、多列／幅狭型は*C. postiae*として新たに種の階級で記載された (Kamiya *et al.* 1997, 1999)。

Kamiya *et al.* (1997, 1999) に従い、Nakhon Si Thammarat（タイ）とGiao Thuy（ベトナム）、Benoa Bay（インドネシア）で採集された標本の節間部の長さと幅、節部中軸細胞から生じる細胞列数を測定した。また、Benoa Bay（インドネシア）の試料には、極端に幅の広い個体と狭い個体が混生していたので、それらはそれぞれ別の個体群として扱った。

その結果、Nakhon Si Thammarat（タイ）とBenoa Bay（インドネシア）の幅の狭い個体群は多列／幅狭型で*C. postiae*、Benoa Bay（インドネシア）の幅の広い個体群は単列／幅広型で*C. monosticha*であると考えられた。しかしGiao Thuy（ベトナム）の標本は、節間部の長さと幅では*C. postiae*と*C. monosticha*の中間に位置し、細胞列数は77％が２、３列で多列であった。この結果は温帯に生育する*C. continua*に似ているが、*C. continua*とは細胞列数のほとんど４列以上である点で異なる。そのため、Giao Thuy（ベトナム）産の標本は同定が困難であり、*Caloglossa* sp. として記録した。

タイ・ベトナム・フィリピン・インドネシアの出現種

	Thailand			Vietnam				Philippines		Indonesia				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Catenella nipae									+	+	+		+	
C. impudica										+				
C. sp.													+	
Bostrychia tenella												+		
B. binderi									+				+	
B. radicans	+	+	+		+		+				+		+	
B. moritziana	+													
Stictosiphonia kelanensis							+	+			+		+	
S. hookeri		+	+	+										
Caloglossa bengalensis			+	+	+									
C. adhaerens	+	+	+	+	+		+	+		+	+		+	
C. ogasawaraensis	+	+	+	+	+	+	+			+	+		+	
C. beccarii					+									
C. leprieurii	+				+	+	+			+	+		+	
C. monosticha										+	+		+	
C. postiae	+	+	+				+		+	+	+		+	
C. sp.				+										

1. Nakhon Si Thammarat, Thailand, 2. East Surat Thani, Thailand, 3. Tapee River, Surat Thani, Thailand, 4. Giao Thuy, Vietnam, 5. Can Gio, Vietnam, 6. Dong Nai River, Ho Chi Minh, Vietnam, 7. Bolinao, Luzon Isl., Philippines, 8. Wawa River, Batangas, Luzon Isl., Philippines, 9. Mactan Isl., Cebu Isl., Philippines, 10. Benoa Bay, Bali, Indonesia, 11. Serangan Isl., Benoa Bay, Bali, Indonesia, 12. Jimbaran, Bali, Indonesia, 13. Gilimanuk, Bali, Indonesia, 14. Labuhan Lalang, Bali, Indonesia

以下に，本研究で採集された標本の番号と採集地，採集日時をあげる。

標本番号	採集地	採集日
タイ		
7722	Nakhon Si Thammarat (mangrove)	1999/5/6
7723	Nakhon Si Thammarat (mangrove)	1999/5/6
7724	Nakhon Si Thammarat (mangrove)	1999/5/6

7725	East Surat Thani (mangrove)	1999/5/7
7726	East Surat Thani (mangrove)	1999/5/7
7727	East Surat Thani (mangrove)	1999/5/7
7728	East Surat Thani (mangrove)	1999/5/7
7729	East Surat Thani (mangrove)	1999/5/7
7730	East Surat Thani (mangrove)	1999/5/7
7733	East Surat Thani (mangrove)	1999/5/7
7734	East Surat Thani (mangrove)	1999/5/7
7735	East Surat Thani (mangrove)	1999/5/7
7736	Tapee River (mangrove), Surat Thani	1999/5/7
7737	Tapee River (mangrove), Surat Thani	1999/5/7
7738	Tapee River (mangrove), Surat Thani	1999/5/7
ベトナム		
7741	Giao Thuy (mangrove)	2000/7/18
7742	Giao Thuy (mangrove)	2000/7/18
7748	Giao Thuy (mangrove)	2000/7/18
7749	Giao Thuy (mangrove)	2000/7/19
7750	Giao Thuy (mangrove)	2000/7/19
7751	Giao Thuy (mangrove)	2000/7/19
7752	Giao Thuy (mangrove)	2000/7/19
7753	Giao Thuy (mangrove)	2000/7/20
7754	Giao Thuy (mangrove)	2000/7/21
7756	Giao Thuy (mangrove)	2000/7/21
7757	Giao Thuy (mangrove)	2000/7/21
7758	Giao Thuy (mangrove)	2000/7/21
7759	Giao Thuy (mangrove)	2000/7/21
7760	Giao Thuy (mangrove)	2000/7/21
7761	Can Gio (mangrove)	2000/7/25
7762	Can Gio (mangrove)	2000/7/25
7763	Can Gio (mangrove)	2000/7/25
7764	Can Gio (mangrove)	2000/7/25
7766	Can Gio (mangrove)	2000/7/25
7767	Can Gio (mangrove)	2000/7/25
7768	Can Gio (mangrove)	2000/7/25
7771	Can Gio (mangrove)	2000/7/25
7772	Can Gio (mangrove)	2000/7/25
7773	Can Gio (mangrove)	2000/7/25
7774	Can Gio (mangrove)	2000/7/25
7775	Can Gio (mangrove)	2000/7/25
7776	Can Gio (mangrove)	2000/7/25
7777	Can Gio (mangrove)	2000/7/27
7778	Can Gio (mangrove)	2000/7/27
7780	Can Gio (mangrove)	2000/7/27
7782	Can Gio (mangrove)	2000/7/27
7783	Can Gio (mangrove)	2000/7/27
7784	Can Gio (mangrove)	2000/7/27
7785	Can Gio (mangrove)	2000/7/27
7786	Can Gio (mangrove)	2000/7/27
7787	Can Gio (mangrove)	2000/7/27

8046	Giao Thuy (mangrove)	2000/7/19
8047	Giao Thuy (mangrove)	2000/7/19
8048	Dong Nai River	2000/7/28
フィリピン		
8050	Bolinao (mangrove), Luzon Is.	2000/12/12
8051	Bolinao (mangrove), Luzon Is.	2000/12/12
8052	Bolinao (mangrove), Luzon Is.	2000/12/12
8053	Bolinao (mangrove), Luzon Is.	2000/12/12
8054	Bolinao (mangrove), Luzon Is.	2000/12/12
8055	Bolinao (mangrove), Luzon Is.	2000/12/13
8056	Bolinao (mangrove), Luzon Is.	2000/12/13
8057	Bolinao (mangrove), Luzon Is.	2000/12/13
8058	Bolinao (mangrove), Luzon Is.	2000/12/13
8059	Bolinao (mangrove), Luzon Is.	2000/12/14
8060	Bolinao (mangrove), Luzon Is.	2000/12/14
8061	Bolinao (mangrove), Luzon Is.	2000/12/14
8062	Bolinao (mangrove), Luzon Is.	2000/12/14
8063	Bolinao (mangrove), Luzon Is.	2000/12/14
8064	Wawa River, Batangas, Luzon Is.	2000/12/16
8065	Wawa River, Batangas, Luzon Is.	2000/12/17
8066	Mactan Is. (mangrrove)., Cebu Is.	2000/12/19
8067	Mactan Is. (mangrrove)., Cebu Is.	2000/12/19
8068	Mactan Is. (mangrrove)., Cebu Is.	2000/12/19
8069	Mactan Is. (mangrrove)., Cebu Is.	2000/12/19
8070	Mactan Is. (mangrrove)., Cebu Is.	2000/12/19
8071	Mactan Is. (mangrrove)., Cebu Is.	2000/12/19
8072	Mactan Is. (mangrrove)., Cebu Is.	2000/12/19
インドネシア		
8260	Benoa Bay (mangrove), Bali	2001/8/26
8261	Benoa Bay (mangrove), Bali	2001/8/26
8262	Benoa Bay (mangrove), Bali	2001/8/26
8263	Benoa Bay (mangrove), Bali	2001/8/26
8264	Benoa Bay (mangrove), Bali	2001/8/26
8265	Jimbaran(beach), Bali	2001/8/26
8266	Benoa Bay (mangrove), Bali	2001/8/26
8267	Benoa Bay (mangrove), Bali	2001/8/26
8268	Jimbaran(beach), Bali	2001/8/26
8269	Benoa Bay (mangrove), Bali	2001/8/26
8270	Benoa Bay (mangrove), Bali	2001/8/26
8271	Benoa Bay (mangrove), Bali	2001/8/26
8272	Benoa Bay (mangrove), Bali	2001/8/26
8273	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8274	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8275	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8276	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8277	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8278	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8279	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8280	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27

8281	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8282	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8283	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8284	Serangan Is., Benoa Bay (mangrove), Bali	2001/8/27
8285	Gilimanuk (mangrove), Bali	2001/8/29
8286	Gilimanuk (mangrove), Bali	2001/8/29
8287	Gilimanuk (mangrove), Bali	2001/8/29
8288	Gilimanuk (mangrove), Bali	2001/8/29
8289	Labuhan Lalang (mangrove), Bali	2001/8/29
8290	Benoa Bay (mangrove), Bali	2001/8/31
8291	Benoa Bay (mangrove), Bali	2001/8/31

塚越　哲・池谷仙之：介形虫類の生物地理

貝形虫類に関する報告

研究史

東南アジア周辺の海生貝形虫類の研究は、今日まで船舶から試料採集をする浅海域の生物相を記載する研究がほとんどであり、Brady（1868）によるジャワ島周辺の貝形虫類相の記載にはじまる。Brady（1869）は、翌年、香港からも貝形虫類を報告し、つづいて「チャレンジャー・レポート」でジャワ、フィリピンからの報告を行った（Brady, 1880）が、その後20世紀半ばまではこの地域での研究はなされなかった。20世紀に入ってから、Kingma（1948）がインドネシア諸島の地層（中新世中期から鮮新世後期）から化石貝形虫類の記載を行い、また Keij（1954）がフィリピン周辺の貝形虫類の記載をした。1980年代以降、東南アジアの貝形虫類相に関する研究が相次いだ。まず、東シナ海を Wang & Zhao (1985)によって、マラッカ海峡を Whatley & Zhao (1987, 1988) が、マレー半島の河川および内湾部を Zhao & Whatley(1989)が、またシンガポールとカリマンタン島西端間の陸棚を Mostafawi(1992)が報告した。陸棚以外では、Whatley & Watson (1988)がサンゴ礁、Whatley（1992）が、西太平洋の水深1,200m－4,200mの海底の貝形虫類を報告したが、いずれも予察的なもので、貝形虫類相としての記載はなされていない。特定の分類群については、*Neosinocythere*、*Krithe*、*Parakrithe*、*Glyphidocythere*、*Eucytherura*、*Hemiparacytheridea* 等の記載報告がある。

問題点と本研究の役割

本地域における貝形虫研究は、Whatley & Watson (1988)を除き、船舶を用いて底質試料を採集したものである。そのため、種多様性の高い潮間帯に棲む貝形虫類の報告は皆無に近い。また、これまでの研究は、堆積物中に残る貝形虫類の遺骸を扱うという特性から、すべて石灰質の背甲形質のみの記載報告であり、分類学的に多くの情報を有する付属肢や交尾器などの軟体部についての記載が欠落している。

本研究では、タイ、マレーシア、ベトナム、フィリピン、インドネシアにおいて、生体標本を得るために潮間帯を中心とした試料採取を行い、試料は乾燥試料と液浸試料とに分けて保存された。液浸試料は、軟体部観察のために適した標本を抽出することができる。これにより、潮間帯生貝形虫類について、種レベルでの分類・記載を高い精度で行い、本地域内外の貝形虫類の比較研究を行って、生物地理的な考察をすることを目的としている。また、本地域では手付かずのままになっている間隙性貝形虫類の試料も採集したので、これについても今後記載してゆく。

タイおよびマレーシア（1999年5月および11-12月）

生体として産出した種は少なく、ほとんどが遺骸として背甲のみが産出した。但しまだ検鏡が終了していない試料も多数あるので、今後新たに付け加わる可能性は残されている。4種中3種は、フィリピンと共通している。

遺骸群集としては非常に種多様性が高く、船舶で採集された Mostafawi (1992)で報告された群集と共通する種が多い。これは多くの貝形虫類の生活場所が、潮間帯よりも深いところにあることを意味している可能性がある。生体として（軟体部付で）産出した種は以下に示す4属4種が確認された。

Loxoconcha illijeborgii (Brady, 1868) [991119-1]
Mutilus? varionatus (Hartmann, 1978) [991119-1]
Tanella glacilis (Kingma, 1948) [991119-1]
Xestoleberis sp. 1 (hanaii-type) [991119-1, 5-3-2]

[ ]内は産出した試料番号（以下同じ）

ベトナム（2000年7月）

試料採集のほとんどは、ラグーンやマングローブ湿地帯等、塩濃度の低い水域において行われた。これらの水域では貝形虫類相はきわめて貧相（多くは遺骸のみ産出）である。遺骸を含めた

貝形虫類相としては、Mostafawi (1992)で報告された分類群と共通するものが多い。生体として（軟体部付で）産出した種は以下に示す9属12種が確認された。

Alocopocythere? sp. 1 [000719-2]
Callistocythere sp. 1* [000719-2]
Caudites sp. 1 [000728-3]
Hemicytheridea cancellata (Brady, 1868) [000719-2]
Loxoconcha georgei Hartman, 1978 [000728-3]
Loxoconcha sp. 1 [000719-2, 000720-2]
Mutilus? varionatus (Hartmann, 1978) [000728-3]
Neomonoceratina sp. 1 [000726-3]
Pontocythere sp. 1 [000728-3]
Tanella glacilis (Kingma, 1948) [000719-2]
Tanella sp. 1* [000725-1]
Tanella sp. 2* [000726-3]

*印は、未記載種である可能性が特に高いもの（以下同じ）

フィリピン（2000年12月）

生体として（軟体部付で）産出した種は以下に示すとおり、13属16種が確認された。このうち2種は赤道を挟んでオーストラリア北部まで分布が広がっている。また、日本国内と共通種は見られなかったが、属レベルでは、13属中9属が共通していた。

Bairdoppilata portsamsonensis Hartmann, 1978 [001214-5]
Caudites sp. 2 [001214-2, 001214-3, 001214-5]
Cyprideis? sp. 1 [001212-5, 001216-1]
Cytheromorpha sp. 1* [001212-3]
Loxoconcha sp. 2 (ura-type) [001212-5]
Miocyprideis spinulosa (Brady, 1868) [001212-4]
Mutilus? varionatus (Hartmann, 1978) [001214-2, 001214-5, 001214-9]
Mutilus? sp. 1 (spine-type) [001214-9]
Neonesidea sp. 1 (elongate-type) [001214-9]
Parakurithella sp. [001212-4, 001212-5]
Propontocypris sp. [001212-5, 001214-2, 001216-1, 001216-2]
Spinileberis sp. 1* [001212-3, 001212-4, 001212-5]
Tanella glacilis (Kingma, 1948) [001212-4, 001214-3]
Tanella sp. 1* [001214-2, 001214-3]
Xestoleberis sp. 1 (hanaii-type) [001212-4, 001214-2, 001214-5]
Xestoleberis sp. 2 (flat-type) [001214-9]

インドネシア（2000年8-9月）

タイ（マレーシア）、ベトナム、フィリピンに比べ、外洋性環境での採集地点が多く、種多様性も高い。以下に示す12属22種が、生体（軟体部付）で確認された。このうち4種は、オーストラリア北部からHartmann(1978)によって報告されたものと一致した。

Callistocythere sp. 1 (small/kobu-type) [010904-1]
Caudites exmouthensis Hartmann, 1978 [010904-5]
Caudites sp. 2 [010831-2]
Caudites sp. 3 [010830-2]
Cytherelloidea koegleri Mostafawi, 1992 [010904-1]
Keijia borneoensis Mostafawi, 1992 [010904-1]
Loxoconcha georgei Hartmann, 1978 [010830-2, 010904-2]
Loxoconcha illijeborgii (Brady, 1868) [010830-2]
Macrocypris sp. 1 [010831-2]
Mutilus? australiensis Hartamann, 1978 [010830-2, 010904-1]
Mutilus? varionatus (Hartmann, 1978) [010830-2, 010831-2, 010904-1, 010904-2]
Mutilus? sp. 1 (spine-type) [010904-5]
Mutilus? sp. 2 (fossa-type) [010831-1]
Neonesidea sp. 2 [010831-2, 010904-5]

Paradoxostoma sp 1. (maru/kuro-type) [010831-1, 010831-2]
Paradoxostoma sp. 2 (maru/ki-type) [010831-1, 010831-2]
Tanella sp. 2 [010902-1, 010904-2]
Triebelina sp. 1 [010904-1]
Xestoleberis sp. 1 (hanaii-type) [010831-2, 010904-1]
Xestoleberis sp. 2 (flat-type) [010831-2]
Xestoleneris sp. 3 (maru-tpe) [010903-3, 010904-5]
Xestoleberis sp. 4 (daen/kuro-type) [010904-1]

まとめ

タイ／マレーシア、ベトナム、フィリピン、インドネシア各地域間の類似度を考察すると、未検鏡の試料が存在するため結論することはできないが、上記データーの範囲内では、インドネシアとフィリピン間で 5 種が共有されて最大である。また、インドネシアは、オーストラリア北部と 4 種を共有している。もちろん、タイ／マレーシアで未検鏡試料が多いこと、ベトナムではラグーン性の地域が多かったことなどを考慮すれば、この結果をそのまま受け入れることはできない。

種レベルでの同定のためには、何れの種も軟体部の解剖学的情報が必要であり、今後解剖を進めてゆく予定である。また、背甲形質のみで記載された既知種については、軟体部形質をふくめた再記載が必要で、そのためにはタイプ標本と比較が必須となる。

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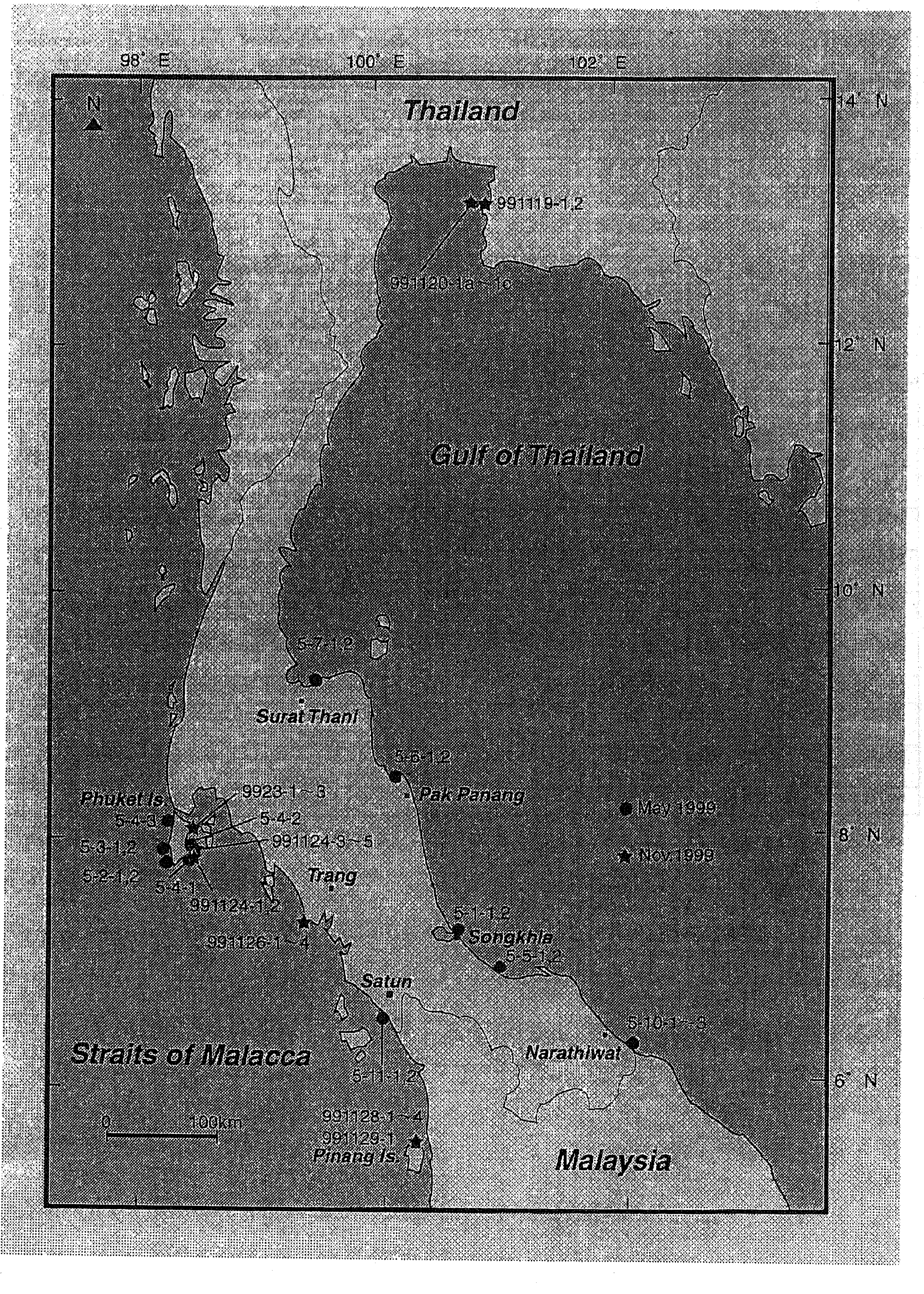
タイ　貝形虫サンプルリスト

Sample No.	Date (1999)	Locality Name	Depth (cm)	Environment, Type of Sa,ple / Sampling Instrument or Type of Samples
5-1-1	May 1	Mouth of Thale Sap Songkhla, Songkhla, Thailand	150	Clay-silt, under jetty / B-net
5-1-2	May 1	Samila Beach, near Songkhla, Thailand	-	Sand among rocks, along sand beach, algae / Hand sampling
5-2-1	May 2	N of Karon Noi Beach, Relax Bay, S-W of Phuket Is., Thailand	150	Sand among rocks, rocky shore / H-net
5-2-2	May 2	N of Karon Noi Beach, Relax Bay, S-W of Phuket Is., Thailand	-	Gravely beach, algae attached on gravels / Hand sampling
5-3-1	May 3	Ka Lim Beach, S-W of Phuket Is., Thailand	-	Sand among corals / H-net
5-3-2	May 3	Ka Lim Beach, S-W of Phuket Is., Thailand	100	Tide pool, rocky shore, algae / Hand sampling
5-4-1	May 4	Cape Panwa, S-E of Phuket Is., Thailand	900	Clay with shell sand, under jetty / B-net
5-4-2	May 4	Mai Phai Cape Bamboo, E of Si-Rae Is., S-E of Phuket Is., Thailand	30	Sand beach / H-net
5-4-3	May 4	100 m off Nai Yang Beach, N-W of Phuket Is.,Thailand	50-150	Sand among corals / H-net
5-5-1	May 5	Kham Is., 30 km S-E of Phuket Is., Thailand	100	Coral reef, algae / Hand sampling
5-5-2	May 5	500 m W off Kham Is., 30 km S-E of Songkhla, Thailand	700	Silt with shell sand, strait / B-net
5-6-1	May 6	500 m off Phanang Bay, Pak Phanang, Thailand	50	Clayey sand, mouth of lagoon / B-net
5-6-2	May 6	100 m off Phanang Bay, Pak Phanang, Thailand	50	Clayey sand, mouth of lagoon / B-net
5-7-1	May 7	Mouth of Chaber Channel, Takien Tong, Surat Thani, Thailand	-	Clay with shell fragments, lagoon / H-net
5-7-2	May 7	Mouth of Ta Pi River, Ban Pak Nam, Surat Thani, Thailand	300	Clay, Mangrove / B-net
5-10-1	May 10	Tak Bai Beach, Ban Sala Mai, 3.4 km S-E of Narathiwat, Thailand	300-400	Sand near rocky pier / B-net
5-10-2	May 10	Tak Bai Beach, Ban Sala Mai, 3.4 km S-E of Narathiwat, Thailand	-	Sand beach / H-net
5-10-3	May 10	Tak Bai Beach, Ban Sala Mai, 3.4 km S-E of Narathiwat, Thailand	400	Under bridge on cultural pond / B-net
5-11-1	May 11	Mouth of Tha Chin River, S of Satun, Thailand	-	Clay, mangrove swanp / B-net
5-11-2	May 11	Off Tha Chin Bay, S of Satun, Thailand	1000	Clay / B-net
991119-1	Nov. 19	Near Marine stationm E of Si Chang Is., 77 km S0e of Bangkok, Thailand	-	Tide pool, rocky shore / H-net
991119-2	Nov. 19	Near Marine stationm E of Si Chang Is., 77 km S0e of Bangkok, Thailand	-	Sand beach / H-net
991120-1a	Nov. 20	Tam Pang beach, W of Si Chang Is., Thailand	-	Sand among Mytilus bed / H-net
991120-1b	Nov. 20	Tam Pang beach, W of Si Chang Is., Thailand	-	Tide pool / H-net
991120-1c	Nov. 20	Tam Pang beach, W of Si Chang Is., Thailand	50	Sand among rocks, sublitoral zone / H-net
991123-1	Nov. 23	Mouth of Laem Yang, N-E of Phuket Is. , Thailand	100	C-sand, Mangrove B-net
991123-2	Nov. 23	200 m off Hin Bang Sai, N-E of Phuket Is., Thailand	30	Seagrass bed / H-net
991123-3	Nov. 23	100 m off Hin Bang Sai, N-E of Phuket Is., Thailand	5	Seagrass (*Enhalus acoroides*) bed / H-net
991124-1	Nov. 24	Cape Panwa, S-E of Phuket Is., Thailand	-	Seagrass (*Cymodocea rotumdata*) bed / H-net
991124-2	Nov. 24	Cape Panwa, S-E of Phuket Is., Thailand	-	Coral Reef, c. sand among corals / H-net
991124-3	Nov. 24	Leam Phap Pha, S-E of Phuket Is., Thailand	50	Coral reef, c-m. sand among corals / H-net
991124-4	Nov. 24	Leam Phap Pha, S-E of Phuket Is., Thailand	20	Coral reef, c. sand among dead corals / H-net
991124-5	Nov. 24	Leam Phap Pha, S-E of Phuket Is.,	1-2	Mudflat / H-net

		Thailand		
991126-1	Nov. 25	Ban Khuan, Tung Ku, 3.5 km S-E of Trang, Thailand	2	Mangrove, mud flat / Y-spoon
991126-2	Nov. 25	Leam Yong Lam, Ban Ko Muk, 3.5 km S-E of Trang, Thailand	-	Seagrass bed / H-net
991126-3	Nov. 25	Khlong Khuan, 3.5 km S-E of Trang, Thailand	300	Mangrove creek, m-f. sand / B-net
991126-4	Nov. 25	Ban Khuan, Tung Ku, 3.5 km S-E of Trang, Thailand	200	Mangrove creek / B-net
991128-1	Nov. 28	Tanjung Bunga, N coast of Pinang Is., Malaysia	-	Stream mouth, algae with c-m. sand / Hand sampling
991128-2	Nov. 28	Mouth of stream, Tanjung Bunga, N coast of Pinang Is., Malaysia	-	Stream mouth, botom sediments, c-m. sand with detritus / H-net
991128-3	Nov. 28	Tanjung Bunga, N coast of Pinang Is., Malaysia	-	Stream, 20 m upper course from 28-2, muddy sand / h-net
991128-4	Nov. 28	Tanjung Bunga, N coast of Pinang Is., Malaysia	-	Stream, Under bridge, 30 m upper course from 28-3/ H-Net
991129-1	Nov. 29	10 m off Tanjung Bunga, N coast of Pinang Is. , Malaysia	130	Beach, mud / H-Net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5-6-1,2
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Phuket Is.
9923-1 ~ 3
5-4-3
5-4-2
5-3-1,2
991124-3 ~ 5
5-2-1,2
5-4-1
Trang
991124-1,2
991126-1 ~ 4
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Pinang Is.
Malaysia

ベトナム　貝形虫サンプルリスト

Sample No.	Date (2000)	Locality Name	Depth (cm)	Environment, Type of Sample /Sampling Instrument
000719-1	Jul. 19	Quang Thanh Town, Hue Prov.	30	Lagoon, Seagrass bed /H-net
000719-2	Jul. 19	Quang Thanh Town, Hue Prov.	20	Lagoon, Sandy mud /H-net
000719-3	Jul. 19	Thuan An Town, Hue Prov.	20	Lagoon, Mud /H-net
000720-1	Jul. 20	Dam Cau Hai, SE of Hue City	100	Lagoon, Mud /B-net
000720-2	Jul. 20	Dam Cau Hai, SE of Hue City	30	Mouth of lagoon, Sandy mud /H-net
000720-3	Jul. 20	Dam Cau Hai, SE of Hue City	30	Mouth of lagoon, Sandbank, Coarse sand / (IF)
000721-1	Jul. 21	Dam Lang Co	100	Lagoon, Seagrass bed /B-net
000721-2	Jul. 21	Dam Lang Co	30	Mouth of lagoon, Mud / Y-spoon
000721-3	Jul. 21	Dam Lang Co	20	Mouth of lagoon, Sandbeach, Medium Sand / (IF)
000721-4	Jul. 21	Dam Lang Co (east coast)	20	Lagoon, Mud / Y-spoon
000725-1	Jul. 25	Dong Hoa	<5	Mangrove creek of the lower reaches, Mud /Y-spoon
000725-2	Jul. 25	Dong Hoa	<5	Mangrove creek of the middle reaches, Mud / Y-spoon
000725-3	Jul. 25	Dong Hoa	<5	Mangrove creek of the upper reaches, Mud / Y-spoon
000726-1	Jul. 26	Can Cio	20	Fishing port, Outside of levee, Muddy sand / Y-spoon
000726-2	Jul. 26	Can Cio	<5	Fishing port, Inside of levee, Mud / Y-spoon
000726-3	Jul. 26	Can Cio	10	Lagoonal beach, Offshore side, Medium sand / H-net
000726-4	Jul. 26	Can Cio	10	Lagoonal beach, Land side, Medium sand / H-net
000728-1	Jul. 28	Mu Yung Tao, Vung Tau	20	Sandbeach, Medium-coarse sand / (IF)
000728-2	Jul. 28	Mu Yung Tao, Vung Tau	20	Fishing port, Lagoonal beach, Fine sand / H-net
000728-3	Jul. 28	Vung Tau Beach	20	Rocky Shore, Calcarious algae / Hand sampling
000728-4	Jul. 28	Vung Tau Beach	-20	Sandbeach, Fine-medium sand / (IF)

フィリピン　貝形虫サンプルリスト

Sample No.	Date (2000)	Locality Name	Depth (cm)	Environment, Type of Sample /Sampling Instrument
001212-1	Dec. 12	Aguada	50	Near Mangrove flora, Muddy Sand / H-net
001212-2	Dec. 12	Marimpay, near Anda	50	Dead Coral, Sand / H-net
001212-3	Dec. 12	Siepar, near Anda	10	Near small Mangrove flora, Sandy mud / Hand sampling
001212-4	Dec. 12	Siepar, near Anda	10	Seagrass flora, near small Mangrove flora, Muddy sand / H-net
001212-5	Dec. 12	Tilar, Santiago Is.	50	Seagrass bed, Muddy sand / H-net
001213-1	Dec. 13	Tilar, Santiago Is.	50	Coral reef, Seagrass bed, Calcareous medium sand / H-net
001213-2	Dec. 13	Silaqui Is.	50	Coral reef, Seagrass bed, Calcareous medium sand / H-net
001213-3	Dec. 13	Silaqui Is.	20	Coral reef, Sandbeach, Calcareous coarse sand / (IF)
001214-1	Dec. 14	Bolinao Mar. Lab.	20	Mouth of stream, Coarse sand / H-net
001214-2	Dec. 14	Bolinao Mar. Lab.	10	Rocky Shore, Calcarious algae / Hand sampling
001214-3	Dec. 14	Bolinao Mar. Lab.	10	Seagrass bed, fine sand / H-net
001214-4	Dec. 14	Bolinao Mar. Lab.	20	Sandbeach, Coarse sand / (IF)
001214-5	Dec. 14	Parter	20	Rocky Shore, Calcarious algae / Hand sampling
001214-6	Dec. 14	Parter	20	Sandbeach, Coarse sand / (IF)
001214-7	Dec. 14	Parter	20	Sandbeach, Coarse sand / (IF)
001214-8	Dec. 14	Parter	20	Sandbeach, Coarse sand / (IF)
001214-9	Dec. 14	Parter	20	Rocky Shore, Calcarious algae / Hand sampling
001216-1	Dec. 16	Calumpang R., Wawa, Batangas	20	River mouth, near Mangrove flora / H-net
001216-2	Dec. 16	Anilao, Janao Bay, W of Batangas	50	Pebble-beach, Coarse sand / H-net
001216-3	Dec. 16	San Teodoro, Maricaban Strait	30	Sandbeach, Coarse sand / H-net
001216-4	Dec. 16	San Teodoro, Maricaban Strait	20	Sandbeach, Coarse sand / (IF)

インドネシア　貝形虫サンプルリスト

Sample No.	Date (2001)	Locarity Name	Depth (cm)	Environment, Type of Sample / Sampling Instrument
010829-1	Aug. 29	Soka, Bali	<10	Open-sea environment, high tidal level, sediments under Ulva, Amphipoda and Isopoda / Hand sampling
010829-2	Aug. 29	Gilimanuk, Bali	50	Pebbly beach under an embankment, m. sand / H-net.
010829-3	Aug. 29	Gilimanuk, Bali	<10	Tidal flat, m-f. sand with algae / Y-spoon.
010829-4	Aug. 29	Gilimanuk, Bali	<10	Tidal flat, pebbles and fragments of corals / H- net
010829-5	Aug. 29	Labuhan Lalang, Bali	40	Lagoon, f. sand beach / H-net
010829-6	Aug. 29	Labuhan Lalang, Bali	10	Lagoon, minor seagrass bed, fragments of coral / H-net
010830-1 int	Aug. 30	Air Sanih	-	Rounded pebblly beach, exposure of basalt / (IF)
010830-2	Aug. 30	Air Sanih	<10	Sand between rounded pebbles, exposure of basalt / H-net
010831-1	Aug. 31	Nusa Dua, Bali	20	Seagrass and short algae with sediments / Hand sampling
010831-2	Aug. 31	Nusa Dua, Bali	20-30	Offshore side of the above, brown algae on rocky shore (including calcareous algae and sediments) / Hand sampling
010831-3 int	Aug. 31	Nusa Dua, Bali	-	1 m land side of shoreline / (IF)
010831-4	Aug. 31	Nusa Dua, Bali	-	3 m land side of shoreline / (IF)

int				
010831-5	Aug. 31	Nusa Dua, Bali	<10	Mangrove creek, sandy mud / H-net
010902-1	Sep. 2	Likupang, E. of Mando	5	Tidal flats, floculent layer between ripples / Y-spoon
010902-2	Sep. 2	Munte	10-50	Mangrove tidal flat, mud / Y-spoon
010903-1 int	Sep. 3	Batunoa Beach, Kema □	-	1 m land side of shoreline / (IF)
010903-2	Sep. 3	Batunoa Beach, Kema □	50	Fragments of coral, c-sand / H-net
010903-3	Sep. 3	Tandurusa	0-10	Coral beach, short algae with sediments and fragments of coral / H-net
010903-4 int	Sep. 3	Tandurusa	-	50 cm land side of shoreline / (IF)
010904-1	Sep. 4	Batukapal	<10	Open sea, short brown algae with sediments / Hand sampling
010904-2	Sep. 4	Batukapal	<10	Lagoon, Zostella-Halimeda zone f-m. sand / H-net
010904-3 int	Sep. 4	Batukapal	-	1.5 m land side of shoreline / (IF)
010904-4	Sep. 4	Tumpaan	10-20	Creek of river mouth, mud / Y-spoon
010904-5	Sep. 4	Tasik Ria Resort, Mukopa	30-50	Rocky shore, short algae with sediments / Hand sampling

平成１１，１２年度調査報告

平成１１年度　調査報告

（調査地域：タイ、日本からの調査参加者：山口、池谷、田中、向井、塚越；　調査地域：パプアニューギニア：日本からの調査参加者：山口、池谷、向井）

1999 年度調査はインドネシアおよびパプア・ニューギニアを予定した。インドネシアの政情が不安定で，代わりに2000年度に予定していたタイの調査を実施した。１）4月30日～5月15日，山口，池谷，田中（5月10日帰国），タイ・マレー半島中部のアンダマン海およびシャム湾にて共同研究者のアングスパニック博士（Prince of Songkla University）と共同調査。２）9月30日～10月12日，山口，池谷，向井，パプア・ニューギニア調査。３）11月16日～12月2日，向井，塚越，主にタイ（一部マレーシア）・マレー半島南部のアンダマン海およびシャム湾にて調査。

フジツボ類（山口）：外海種（*Tetraclita, Tetraclitella, Tesseropora, Newmanella*）および内湾種でも *Balanus amphitrite, B. variegatus* はマレー半島両岸に分布し，インド一西太平洋に広く分布する。けれどもマングローブに発見された *B. rhizophorae, B. patelliformis* および *B. thailandicus* n. sp. は *B. amphitrite* 種群に属し，マレー半島の限られた地域に分布する。 *B. rhizophorae* および *B. patelliformis* は今まで原記載以後第２番目の発見となり，それらの形態変異や地理的分布および *B.* n. sp.の発見は *B. amphitrite* 種群の進化を理解するために大変重要である（Puspasari, Yamaguchi & Angsupanich 2000a, b, Puspasari, Yamaguchi & Angsupanich 2001）。

介形虫類（池谷・塚越）：タイにて37資料，マレーシアにて5資料，パプア・ニューギニアにて 16 資料を採集し，そのうち 8 資料（タイ）から 21 属 43 種が同定された。主な優占種は *Hemicytheridea cancellata, H. ornata, H. reticulata, Loxoconcha cf. pentoensis, Neomonoceratina inqua, Phlyctenophora orientalis, Tanella* sp.である。

藻類，田中は中央から南部タイのマングローブに卓越するいわゆるボストリチテム群集と呼ばれる次のような汽水性藻類を採集した，*Caloglossa leprieurii, C. continua, Bostrychia tenella, B. radicans, B. moritziana, Stictosiphonia. kelanensis and Catenella. nippae.*

モエビ類，向井はタイでは，３ヶ所の３サンプルで約 200 個体，パプア・ニューギニアでは 6 ヶ所の９サンプルで総計約 1200 個体を採集した。その中には，*Latreutes pigmaeus, Periclimenes indicus,* *Paeneus* sp.などが発見された。特に多く小型のローソクエビ科がパプア・ニューギニアのミルン湾で採集された。多くの種は今まで日本，オーストラリア，パラオなどから報告されてきた。しかし，いくつかの種は他の場所では見られていない種類もあり，まだ研究の途上であるが，生物地理を理解する上で重要な分類群と思われる。

We are going to field trip to Indonesia and Papua New Guinea in 1999. However, we changed field trip to Thailand and Papua New Guinea, because Indonesia was unstable political situation. 1) Yamaguchi, Ikeya and Tanaka researched areas of Andaman Sea and Gulf of Siam of middle Malay Peninsular with Dr. Angsupanich of co-researcher (Prince of Songkla University) from April 30 to May 15. 2) Yamaguchi, Ikeya and Mukai went to field trip to Papua New Guinea from September 30 to October 12. 3) Mukai and Tsukagoshi made an investigation of Gulf of Siam and Andaman Sea of Thailand (including Malaysia in a part) from November 16 to December 2. On barnacles (by Yamaguchi), all open-sea species such as Tetraclita, Tetraclitella, Tesseropora and Newmanella and some embayment species such as Balanus amphitrite and B. variegatus distribute both sides of Malay Peninsular and widely in Indo-west Pacific. However, three species of mangrove barnacles are belonging to the B. amphitrite Group and distribute in restricted areas of the Peninsular. Discovery of B. rhizophorae and B. patelliformis was second record since original description, and their morphological variations and geographic distributions and also discovery of the Balanus n. sp. are very important for understanding of evolution of the B. amphitrite G. (Puspasari, Yamaguchi & Angsupanich 2000 and submitted). On ostracods (by Ikeya and Tsukagoshi), 37 samples in Thailand, 5 in Malaysia and 16 in Papua New Guinea were collected. Twenty-one genera and 43 species identified in 8 samples from Thailand. The dominant species are *Hemicytheridea cancellata*, *H. ornata*, *H. reticulata*, *Loxoconcha* cf. *pentoensis*, *Neomonoceratina inqua*, *Phlyctenophora orientalis*, and *Tanella* sp. On algae, Tanaka collected the brackish water algae so-called "*Bostrychietum*-association" which are composed with dominant species there in the mangrove areas in the middle to south Thailand as follows: *Caloglossa*

(別紙様式13)

平成１１年度科学研究費補助金研究成果報告書概要

1.研究機関番号　１２５０１　2.研究機関名　千　葉　大　学
3.研究種目　基盤研究　Ａ　２　4.研究期間　平成11年度～平成13年度
5.課題番号　１１６９１１７２
6.研究課題名　東南アジア赤道域沿岸性甲殻類の生物地理とその成立過程の研究

7.研究代表者

研　究　者　番　号	研究代表者名	所　属　部　局　名	職　　名
１０１０１１０６	ヤマグチ　トシユキ 山口　寿之	海洋バイオシステム研究センター	教　授

8.研究分担者（所属機関名は，研究代表者の所属機関と異なる場合に記入すること）

研　究　者　番　号	研究分担者名	所 属 機 関 名・所 属 部 局 名	職　　名
５００２２２２３	イケヤ　ノリユキ 池谷　仙之	静岡大学・理学部	教　授
０００１３５９０	ムカイ　ヒロシ 向井　宏	北海道大学・理学部	教　授
３０１６７４９９	タナカ　ジロウ 田中　次郎	東京水産大学・理学部	助教授
９０２１２０５０	ツカゴシ　アキラ 塚越　哲	静岡大学・理学部	助教授

9.研究成果の概要（当該研究期間のまとめ　600字～800字，図　グラフ等は記載しないこと）

1999年度調査はインドネシアおよびパプア・ニューギニアを予定した。インドネシアの政情が不安定で，代わりに2000年度に予定していたタイの調査を実施した。１）4月30日～5月15日，山口，池谷，田中（5月10日帰国），タイ・マレー半島中部のアンダマン海およびシャム湾にて共同研究者のアングスパニック博士（Prince of Songkla University）と共同調査。２）9月30日～10月12日，山口，池谷，向井，パプア・ニューギニア調査。３）11月16日～12月2日，向井，塚越，主にタイ（一部マレーシア）・マレー半島南部のアンダマン海およびシャム湾にて調査。フジツボ類（山口）：外海種（*Tetraclita, Tetraclitella, Tesseropora, Newmanella*）および内湾種でも *Balanus amphitrite, B. variegatus* はマレー半島両岸に分布し，インド一西太平洋に広く分布する。けれどもマングローブに発見された *B. rhizophorae, B. patelliformis* および *B.* n. sp.は *B. amphitrite* 種群に属し，マレー半島の限られた地域に分布する。. *Rhizophorae* および *B. patelliformis* は今まで原記載以後第２番目の発見となり，それらの形態変異や地理的分布および *B.* n. sp.の発見は *B. amphitrite* 種群の進化を理解するために大変重要である（Puspasari, Yamaguchi & Angsupanich 2000, Puspasari, Yamaguchi & Angsupanich 投稿中）。貝形虫類（池谷・塚越）：タイにて37資料，マレーシアにて5資料，パプア・ニューギニアにて16資料を採集し，そのうち8資料（タイ）から21属43種が同定された。主な優占種は *Hemicytheridea cancellata, H. ornata, H. reticulata, Loxoconcha* cf. *pentoensis, Neomonoceratina inqua, Phlyctenophora orientalis, Tanella* sp.である。藻類，田中は中央から南部タイのマングローブに卓越するいわゆるコケモドキ-アヤギヌ群落と呼ばれる次のような汽水性藻類を採集した，*Caloglossa leprieurii, C. continua, Bostrychia tenella, B. radicans, B. moritziana, Stictosiphonia. kelanensis* and *Catenella. nippae*。モエビ類，向井はタイでは，３ヶ所の３サンプルで約200個体，パプア・ニューギニアでは６ヶ所の９サンプルで総計約1200個体を採集した。その中には，*Latreutes pigmaeus, Periclimenes indicus, Paeneus* sp.などが発見された。特に多く小型のローソクエビ科がパプア・ニューギニアのミルン湾で採集された。多くの種は今まで日本，オーストラリア，パラオなどから報告されてきた。しかし，いくつかの種は他の場所では見られていない種類もあり，まだ研究の途上であるが，生物地理を理解する上で重要な分類群と思われる。

10.キーワード

(1)	東南アジア	(2)	甲殻類	(3)	沿岸性
(4)	生物地理	(5)	フジツボ類	(6)	貝形虫類
(7)	モエビ類	(8)	カニ類		

（裏面に続く）

(別紙様式 14)

ABSTRACTS OF RESEARCH PROJECT, GRANT-IN-AID FOR SCIENTIFIC RESEARCH (A 2)

1. RESEARCH INSTITUTION NUMBER: 12501
2. RESEARCH INSTITUTION: Chiba University
3. CATEGORY: A 2
4. TERM OF PROJECT: (1999-2001)
5. PROJECT NUMBER: 11691172
6. TITLE OF PROJECT: Crustacean Biogeography in Equatorial area of Southeast Asia
7. HEAD INVESTIGATOR: 10101106 T. Yamaguchi, Marine Biosystems Research Center, Chiba University Professor
8. INVESTIGATORS (1) 50022223 N. Ikeya, Faculty of Science, Shizuoka University Professor
   (2) 00013590 H. Mukai, Faculty of Science, Shizuoka University Professor
   (3) 0167499 J. Tanaka, Tokyo University of Fisheries Assoc. Prof.
   (4) 90212050 A. Tsukagoshi, Faculty of Science, Shizuoka University Assoc. Prof.

9. SUMMARY OF RESEARCH RESULTS

We are going to field trip to Indonesia and Papua New Guinea in 1999. However, we changed field trip to Thailand and Papua New Guinea, because Indonesia was unstable political situation. 1) Yamaguchi, Ikeya and Tanaka researched areas of Andaman Sea and Gulf of Siam of middle Malay Peninsular with Dr. Angsupanich of co-researcher (Prince of Songkla University) from April 30 to May 15. 2) Yamaguchi, Ikeya and Mukai went to field trip to Papua New Guinea from September 30 to October 12. 3) Mukai and Tsukagoshi made an investigation of Gulf of Siam and Andaman Sea of Thailand (including Malaysia in a part) from November 16 to December 2. On barnacles (by Yamaguchi), all open-sea species such as *Tetraclita, Tetraclitella, Tesseropora* and *Newmanella* and some embayment species such as *Balanus amphitrite* and *B. variegatus* distribute both sides of Malay Peninsular and widely in Indo-west Pacific. However, three species of mangrove barnacles are belonging to the *B. amphitrite* Group and distribute in restricted areas of the Peninsular. Discovery of *B. rhizophorae* and *B. patelliformis* was second record since original description, and their morphological variations and geographic distributions and also discovery of the *Balanus* n. sp. are very important for understanding of evolution of the *B. amphitrite* G. (Puspasari, Yamaguchi & Angsupanich 2000 and submitted). On ostracods (by Ikeya and Tsukagoshi), 37 samples in Thailand, 5 in Malaysia and 16 in Papua New Guinea were collected. Twenty-one genera and 43 species identified in 8 samples from Thailand. The dominant species are *Hemicytheridea cancellata, H. ornata, H. reticulata, Loxoconcha* cf. *pentoensis, Neomonoceratina inqua, Phlyctenophora orientalis,* and *Tanella* sp. On algae, Tanaka collected the brackish water algae so-called "Bostrychietum-association" which are composed with dominant species there in the mangrove areas in the middle to south Thailand as follows: *Caloglossa leprieurii, C. continua, Bostrychia tenella, B. radicans, B. moritziana, Stictosiphonia. kelanensis* and *Catenella. nippae*. On grass-shrimps, Mukai collected 200 shrimps at 3 sites of Thailand, and 1200 shrimps at 6 sites of Papua New Guinea from seagrass meadows. They includes *Latreutes pigmaeus, Periclimenes indicus, Processidae, Paeneus* sp. In particular, many Processid small shrimps were collected from one site of Milne Bay, PNG. Most species have been reported from tropical seagrass beds of Japan, Australia, Belau, etc. However, some species have not been known from those areas, which is poor number in collection, would be key species for understanding biogeography of grass-shrimps in the Indo-West Pacific.

10. KEY WORDS

(1) Southeast Asia (2) Crustacea (3) Littoral
(4) Biogeography (5) Barnacles (6) Ostracods
(7) Shrimps (8) Crabs

(CONTINUE TO NEXT PAGE)

11.研究発表　（発表予定も含む。但し，投稿中，投稿準備中は除く。）

[雑誌論文]

著者名	論文標題
Puspasari, I.A., T. Yamaguchi and S. Angsupanich	Reexamination of a Little-known Mangrove Barnacle, *Balanus patelliformis* Bruguière (Cirripedia, Thoracica) from the Indo-West Pacific.

雑誌名	巻・号	発行年	ページ
Sessile Organisms	16(2)	2000	1-13

著者名	論文標題

雑誌名	巻・号	発行年	ページ

11. REFERENCES

AUTHORS, TITLE OF ARTICLER	JOURNAL, VOLUME-NUMBE PAGES CONCERNED, YEAR
Puspasari, I.A., T. Yamaguchi and S. Angsupanich Reexamination of a Little-known Mangrove Barnacle, *Balanus patelliformis* Bruguière (Cirripedia, Thoracica) from the Indo-West Pacific.	*Sessile Organisms,* 16(2): 1-13, 2000

（様式　８）

平成１２年度科学研究費補助金実績報告書（研究実績報告書）

１．機関番号　1 2 5 0 1

２．研究機関名　千　葉　大　学

３．研究種目名　基盤研究Ａ-２

４．研究期間平成　１１　年度～平成　１３　年度

５．課題番号　1 1 6 9 1 1 7 2

６．研究課題名　東南アジア赤道域沿岸性甲殻類の生物地理とその成立過程の研究

７．研究代表者

研究者番号	研究代表者名	所属部局名	職名
１０１０１１０６	ヤマグチ　トシユキ 山口　寿之	海洋バイオシステム研究センター	教　授

８．研究分担者（所属機関名は，研究代表者の所属機関と異なる場合に記入すること）

研究者番号	研究分担者名	所属機関名・所属部局名	職名
５００２２２２３	イケヤ　ノリユキ 池谷　仙之	静岡大学・理学部	教　授
００１３５９０	ムカイ　ヒロシ 向井　宏	北海道大学・理学部	教　授
３０１６７４９９	タナカ　ジロウ 田中　次郎	東京水産大学・理学部	助教授
９０２１２０５０	ツカゴシ　アキラ 塚越　哲	静岡大学・理学部	助教授

９．研究実績の概要（国立情報研究所でデータベース化するため、６００字～８００字で記入。図、グラフ等は記載しないこと。）

2000年度は7月15日～30日までベトナムでベトナム国立大学P.N. HongおよびD.V. Nhuong教授とハノイ～ホーチミン間の海岸で、また12月10日～20日までフィリピンでフィリピン大学海洋科学研究所のM.D. Fortes教授とルソン島北部ボリナオおよび中部バタンガス、ミンドロ島プエルト・ガレラおよびマクタン島の海岸でマングローブを含む生態系で甲殻類の生物地理の共同調査を実施した。ベトナムでフジツボ類（担当山口）の歴史的研究は無く、全てが新知見となる。特に内湾種の*B. amphitrite*, *B. reticulatus*, *B. kondakovi*, *B. venustus*, *B. variegatus*, *B. rhizophorae*, *B. thailandicus*が特徴的で、最後の２種は今までマレー半島以西にしか知られていない分類群で、新しい地理的分布となる。スナガニ科カニ（担当和田）ベトナム北部では、全部で８属16種で、その内2種が新地理的分布となり、それらの興味深い行動様式が観察された。ベトナム南部では、７属14種が観察された。それらは全て南部からの初記録と思われる。行動の記録としてイワガニ科の中でスナガニ科に近縁とされ*Metaplax crenulata*のwaving displayを記録した。紅藻アヤギヌ類（担当田中）アヤギヌ属は世界中の温帯から熱帯の汽水域に生育し、現在12種が記載されている。マングローブ域における主要な藻類であるが、ベトナムでは今までに報告はされたことがない6種のアヤギヌが確認された。その内*C. leprieurii*は、他地域のものと大きく形態の異なる藻体（*C. leprieurii*矮小型）がベトナムで発見された。貝形虫（担当塚越）ベトナムのラグーンから*Stigmatocythere*属の1種が確認された。その近縁種は、日本の完新世の高海面期に一時的に化石の記録があるが、現在日本近海には生息していない。

※ 成果の公表を見合わせる必要がある場合は、その理由及び差し控え期間等を記入した調書（A4判縦長横き１枚）を添付すること。

１０．キーワード

(1)	東南アジア	(2)	甲殻類	(3)	沿岸性
(4)	生物地理	(5)	フジツボ類	(6)	貝形類
(7)	モエビ類	(8)	カニ類		

（裏面に続く）

１１．研究発表（発表予定を含む。但し、投稿中、投稿準備中は除く。）

〔雑誌論文〕

著　者　名	論文標題
Puspasari, I.A., T. Yamaguchi, and S. Angsupanich	Reexamination of a Little-known Mangrove Barnacle, *Balanus patelliformis* Bruguière (Cirripedia, Thoracica) from the Indo-West Pacific.

雑　誌　名	巻・号	発行年				ページ
Sessile Organisms	16・2	2	0	0	0	1-13

著　者　名	論文標題
Puspasari, I.A., T. Yamaguchi, and S.Kojima	Phylogeny of the *Balanus amphitrite* complex occurring in Japan (Cirripedia: Balanidae) inferred from mitochondrial COI gene and morphology

雑　誌　名	巻・号	発行年				ページ
Sessile Organisms	18・1	2	0	0	1	1-11

著　者　名	論文標題
Asami, K. and T. Yamaguchi	A new coral barnacle, *Trevathana paulayi* (Cirripedia: Pyrgomatidae), from Guam

雑　誌　名	巻・号	発行年				ページ
Sessile Organisms	18・1	2	0	0	1	13-20

著　者　名	論文標題
Puspasari, I.A., T. Yamaguchi, and S. Angsupanich	*Balanus thailandicus* sp. nov., A New Mangrove Barnacle of the *Balanus amphitrite* complex (Cirripedia, Balanomorpha) from Satun, Southwest Thailand

雑　誌　名	巻・号	発行年				ページ
Sessile Organisms	18・1	2	0	0	1	21-28

（様式８）　　平成１３年度科学研究費補助金実績報告書（研究実績報告書）

１．研究機関番号　１２５０１　　２．研究機関名　千葉大学

３．研究種目名　基盤研究　Ａ　２　　４．研究期間　平成１１年度～平成１３年度

５．課題番号　１１６９１１７２

６．研究課題名　東南アジア赤道域沿岸性甲殻類の生物地理とその成立過程の研究

７．研究代表者

研究者番号	研究代表者氏名	所属部局名	職名
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８．研究分担者（所属機関名は、研究代表者の所属機関と異なる場合に記入すること）

研究者番号	研究分担者氏名	所属機関名・所属部局名	職名
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00013590	フリガナ　ムカイ　ヒロシ 向井宏	北海道大学・北方生物圏フィールド科学センター	教授
80127159	フリガナ　ワダ　ケイジ 和田恵次	奈良女子大学・理学部	教授
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90212050	フリガナ　ツカゴシ　アキラ 塚越哲	静岡大学・理学部	助教授

９．研究実績の概要（国立情報学研究所でデータベース化するため、６００字～８００字で記入。図、グラフ等は記載しないこと。）

本年度は、最終年度で、山口、和田、田中、塚越がインドネシア・バリ島、スラウェシ島、西チモール島、ロンボック島、スンバワ島の調査を行った。フジツボ類については、内湾環境に生息する *Balanus amphitrite* 種群に属す、*Balanus amphitrite, B. kondakovi, B. reticulatus, B. variegatus, B. venustus, B. rhizophorae, B. zhujiangensis, B. patelliformis* が知られた。最後の3種 *B. patelliformis, B. rhizophorae, B. zhujiangensis* は歴史的に模式種が採集された場所以外に見つかっていなかったが、新たな分布域が分かった。インド-西太平洋に分布する多くの分類群が発見されたが、オセアニア地域にのみ知られた *Austrobalanus* が唯一パプアニューギニアに発見された。

これまでカニ類の報告がないバリ島全域から、9種のスナガニ科カニ類が確認さら、そのうちの *Tmethypocoelis* 属の1種は、未記載種であることが明らかとなった。同じくこれまでカニ類の報告がないスラウェシ島 Manado 周辺のマングローブ域からは、11種のスナガニ科カニ類が確認され、このうち *Ilyoplax* 属の1種は、フィリピン、ルソン島で本調査により得られた未記載種と同種であり、その Waving 様式も両地域間で同じであることが明らかとなった。本種は、既知種で西大平洋の大陸寄りの地域に分布する *Ilyoplax orientalis* と *Ilyoplax tansuiensis* に、形態的に類似するが、分子系統樹からは、これら既知種の方が本種よりも近縁であることが示唆された。

バリ島において13、スラウェシ島において11、計24の貝形虫用の試料が採取された。このうち6サンプルは間隙性貝形虫類用である。これらのサンプルからは、12属22種が生体（軟体部付）で同定された。このうち2種は未記載種である可能性が高く、また4種は、オーストラリア北部から Hartmann（1978）によって報告された種と同一種である。

※ 成果の公表を見合わせる必要がある場合は、その理由及び差し控え期間等を記入した調書（A4判縦長横き1枚）を添付すること。

１０．キーワード

(1) 東南アジア　(2) 甲殻類　(3) 沿岸性
(4) 生物地理　(5) フジツボ類　(6) 貝形虫類
(7) モエビ類　(8) カニ類

（裏面に続く）

１１．研究発表（印刷中も含む。）

〔雑誌論文〕

著者名	論文標題
Puspasari, I.A., T. Yamaguchi, & S. Kojima	Phylogeny of the *Balanus amphitrite* complex occurring in Japan (Cirripedia: Balanidae) inferred from mitochondrial COI gene and morphology

雑誌名	巻	発行年				ページ
Sessile Organisms	18	2	0	0	1	7 - 17

著者名	論文標題
Asami, K. & T. Yamaguchi	A new coral barnacle, *Trevathana paulayi* (Cirripedia: Pyrgomatidae), from Guam

雑誌名	巻	発行年				ページ
Sessile Organisms	18	2	0	0	1	19 - 26

著者名	論文標題
Puspasari, I.A., T. Yamaguchi, & S. Angsupanich	*Balanus thailandicus* sp. nov., A New Mangrove Barnacle of the *Balanus amphitrite* complex (Cirripedia, Balanomorpha) from Satun, Southwest Thailand

雑誌名	巻	発行年				ページ
Sessile Organisms	18	2	0	0	1	27 - 33

著者名	論文標題
Ross, A. & T. Yamaguchi	Site Selection Wall Development and Biogeography of *Galkinia indica*, an Indo-west Pacific Coral-Inhabiting Barnacle

雑誌名	巻	発行年				ページ
Biogeography	3	2	0	0	1	59 - 68

著者名	論文標題
Puspasari, I.A., T. Yamaguchi, & A. Ross	New record of *Balanus zhujiangensis* Ren, 1989 (Cirripedia, Balanidae) from Okinawa, Japan

雑誌名	巻	発行年				ページ
Journal of Crustacean Biology	22	2	0	0	2	235 - 240

著者名	論文標題
Horii, T., J. Kitaura, K. Wada, & M. Nishida	Genetic relationship among Japanese sentinel crabs (Decapoda: Ocypodidiae: genus *Macrophthalmus*)

雑誌名	巻	発行年				ページ
Comparative Biochemistry and Physiology, Part B,	130	2	0	0	1	75 - 82

著者名	論文標題
Kitaura, J., M. Nishida, & K. Wada	Genetic and behavioral diversity in the *Macrophthalmus japonicus* species complex (Crustacea: Brachyura: Ocypodidae)

雑誌名	巻	発行年				ページ
Marine Biology	140	2	0	0	2	1 - 8

〔図書〕

著者名	出版社

書名	発行年				総ページ数

１２．研究成果による工業所有権の出願・取得状況

工業所有権の名称	発明者名	権利者名	工業所有権の種類、番号	出願年月日	取得年月日

(別紙様式１３)

ABSTRACTS OF RESEARCH PROJECT, GRANT－IN－AID FOR SCIENTIFIC RESEARCH (A－2)

1. RESEARCH INSTITUTION NUMBER; 12501

2. RESEARCH INSTITUTION; Chiba University

3. CATEGORY; A-2

4. TERM OF PROJECT (1999 ～ 2001)

5. PROJECT NUMBER; 11691172

6. TITLE OF PROJECT; Crustacean Biogeography in Equatorial area of Southeast Asia

7. HEAD INVESTIGATOR REGISTERED NUMBER, NAME, INSTITUTION, DEPARTMENT, TITLE OF POSITION

	10101106	T. Yamaguchi	Marine Biosystems Research Institute, Chiba Univ.	Professor
8. INVESTIGATORS	(1) 50022223	N. Ikeya	Faculty of Science, Shizuoka Univ.	Professor
	(2) 00013590	H. Mukai	Center for Northern Biosphere, Hokkaido Univ.	Professor
	(3) 80127159	K. Wada	Faculty of Science, Nara wormen's Univ	Professor
	(4) 30167499	J. Tanaka	Tokyo University of Fisheries	Professor
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9. SUMMARY OF RESEARCH RESULTS

This is the final year for field research on Crustacean Biogeography in Equatorial area of Southeast Asia. Yamaguchi, Wada, Tanaka, and Tsukagoshi had a field trip to Bali, Sulawesi, West Timor, Lombok, and Sumbawa Islands of Indonesia. In the *Balanus amphitrite* complex, *B. amphitrite, B. kondakovi, B. reticulatus, B. variegatus, B. venustus, B. rhizophorae, B. zhujiangensis,* and *B. patelliformis* were found in the area. The last three species, *B. patelliformis, B. rhizophorae,* and *B. zhujiangensis* have never been found except for those type localities, in our field trip we can find them and those biogeographic distributions are new to science. We could find many taxa of barnacles found in the Indo-West Pacific, however, *Austrobalanus* that has been only known in region of Oceania is found at the Papua New Guinea.

Nine species of the family Ocypodidae have been recorded from Bali. Among them, one species of the genus *Tmethypocoelis* has been found to be an undescribed species. Eleven species of Ocypodidae have been recorded from northern Sulawesi. Among them, one species of the genus *Ilyoplax* has been found to be an undescribed species that was also collected in Luzon of the Philippines. This species is morphologically similar to two congeneric species of *I. orientalis* and *I. tansuiensis,* which are distributed in continental coast of the western Pacific. Molecular phylogenetic analysis has revealed that *I. orientalis* and *I. tansuiensis* are more related to each other than to the undescribed species.

Twenty-four samples (13 from Bali Is. and 11 from Sulawesi Is.) were collected for study on Ostracoda. Six of them were for interstitial fauna. Twelve genera and twenty-two species were identified with soft parts. The two species of them must be undescribed species and the four of them are common to the species reported by Hartmann (1978) from Australia.

10. KEY WORDS

(1) Southeast Asia (2) Crustacea (3) Littoral

(4) Biogeography (5) Barnacles (6) Ostracods

(7) Shrimps (8) Crabs

(CONTINUE TO NEXT PAGE)

11. REFERENCES

AUTHORS,TITLE OF ARTICLE	JOURNAL, VOLUME-NUMBER, PAGES, CONCERNED, YEAR
Puspasari, I.A., T. Yamaguchi, & S. Kojima: Phylogeny of the *Balanus amphitrite* complex occurring in Japan (Cirripedia: Balanidae) inferred from mitochondrial COI gene and morphology	*Sessile Organisms,* 18: 7 – 17 (2001)
Asami, K. & T. Yamaguchi: A new coral barnacle, *Trevathana paulayi* (Cirripedia: Pyrgomatidae), from Guam	*Sessile Organisms,* 18: 19 – 26 (2001)
Puspasari, I.A., T. Yamaguchi, & S. Angsupanich: *Balanus thailandicus* sp. nov., A New Mangrove Barnacle of the *Balanus amphitrite* complex (Cirripedia, Balanomorpha) from Satun, Southwest Thailand	*Sessile Organisms,* 18: 27 – 33 (2001)
Ross, A. & T. Yamaguchi: Site Selection Wall Development and Biogeography of *Galkinia indica*, an Indo-west Pacific Coral-Inhabiting Barnacle	*Biogeography,* 3:59-68 (2001)
Puspasari, I.A., T. Yamaguchi, & A. Ross: New record of *Balanus zhujiangensis* Ren, 1989 (Cirripedia, Balanidae) from Okinawa, Japan	*Journal of Crustacean Biology*, 22: 235-240 (2002)
Horii, T., J. Kitaura, K. Wada, and M. Nishida: Genetic relationship among Japanese sentinel crabs (Decapoda: Ocypodidiae: genus *Macrophthalmus*).	*Comparative Biochemistry and Physiology, Part B*, 130: 75-82 (2001)
Kitaura, J., M. Nishida, and K. Wada: Genetic and behavioral diversity in the *Macrophthalmus japonicus* species complex (Crustacea: Brachyura: Ocypodidae).	*Marine Biology*, 140: 1-8 (2002)

SESSILE ORGANISMS 16 (2) 1-13, 2000

Reexamination of a Little-known Mangrove Barnacle, *Balanus patelliformis* BRUGUIÈRE (Cirripedia, Thoracica) from the Indo-West Pacific

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(Received July 10, 1999)

A species, *Balanus patelliformis* BRUGUIÈRE, 1789 belonging to the group of *B. amphitrite* DARWIN group, has been infrequently mentioned in the literature in recent years. It is known from three species of mangrove plants and associated molluscan shells. It is in need of a supplementary descriptions of the wall, opercular plates, mouthparts, and cirri because two species were subsequently described that are more or less closely related. They, *B. kondakovi* TARASOV & ZEVINA, 1957, *B. albicostatus* PILSBRY, 1916, as well as *B. improvisus* DARWIN, 1854 are compared relatively to their phylogenetic relationships. *Balanus patelliformis* is distinguishable from them by the pentagonal shape of the shell, and combinations of other external and internal characters. It is concluded *B. patelliformis* is closely related to *B. albicostatus* and *B. kondakovi*.

In his monograph on the sessile Cirripedia, DARWIN (1854: 259) gave a description of the external morphology of *Balanus patelliformis* BRUGUIÈRE, 1789 (=*B. patellaris* GMELIN, 1790) from the south coast of India.

Supplementary descriptions of this species, with figures of opercular plates and the mouthparts, have been published by NILSSON-CANTELL (1929) and FERNANDO (1978) based on specimens from Rangoon, Burma (now Yangon, Myanmar), and Porto Nova, India, respectively. UTINOMI (1968) described the opercular valves of specimens from the Strait of Malacca. Despite these studies, characteristics of taxonomic importance, such as the presence of subsidiary parietal tubes, a vesicular sheath, and complex setae are not yet known.

During studies by ANGSUPANICH and HAVANONA's (1996) on mangrove seedling restoration in a mangrove estuary (Ban Don Bay, Surat Thani, Thailand) the most abundant barnacles attaching to the stems and leaves of *Avicennia alba*, *Sonneratia caseolaris*, and *Rhizophora mucronata* was referable to *B. patelliformis*. In this paper, the morphological characteristics of *B. patelliformis* are described based on material mentioned below. Comparisons of the shell structure, opercular plates, mouthparts, cirri, and basidorsal point of the penis are made between this and related species in the *B. amphitrite* group.

Materials and Methods

The 23 specimens of *B. patelliformis* examined in this study were collected from Ban Don Bay, Surat Thani, Thailand (9° 19′ 20″ N, 99° 14′ E) by one of us (SA) on September 8, 1997. Most were preserved in 95% ethanol. Measurements of the shell wall sizes and opercular plates were made to the nearest 0.1 mm

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Key words: *Balanus patelliformis*, morphology, phylogeny

using a caliper with a vernier scale. The soft parts including cirri, mouthparts, and penis were dissected, mounted in Kaiser's glycerin jelly, and examined under stereo and compound light microscopes.

Morphological terms in the present study are those adopted by NEWMAN *et al.* (1969), HENRY and McLAUGHLIN (1975), and NEWMAN and ROSS (1976). All specimens examined have been deposited in the National Science Museum, Tokyo, Japan. The registered numbers of those specimens are listed after the Literature cited (p. 12).

Systematics

Balanus patelliformis BRUGUIÈRE, 1789

Type locality: South coast of India.

[Die Stern-patellenförmige Meereichel] SPENGLER, 1780: 106, Pl. 5, Fig. 4; CHEMNITZ, 1785: 316, Pl. 98, Fig. 839.

Balanus patelliformis BRUGUIÈRE, 1789–1792: 60–67; 158–173, Pls. 164–166.

Lepas patellaris GMELIN, 1790: 3213.

Balanus patellaris: DARWIN, 1854: 259, Pl. 6, Figs. 5a–c; GRUVEL, 1905: 238, Fig. 265; NILSSON-CANTELL, 1921: 328; NILSSON-CANTELL, 1929: 4, Figs 1a, b, 3a–f; NILSSON-CANTELL, 1938: 46, Pl. 1, Figs 4, 5; UTINOMI, 1968: 174, Figs 5, 6a, b; NEWMAN & ROSS, 1976: 64.

Balanus patelliformis, BRUGUIÈR: LAMY & ANDRÉ, 1932: 132; HENRY and McLAUGHLIN, 1975: 141, Pls. 16, 17.

Balanus sp.: ANGSUPANICH and HAVANONA, 1996: 78 (=*B. patelliformis*)

As can be seen in the foregoing synonymy, BRUGUIÈRE (1789) utilized part of SPENGLER's (1780) descriptive name ("patellenförmige") in forming a proper Linnean specific name, for the present species (*Balanus patelliformis*). This was overlooked by GMELIN (1790), who again named the species, albeit with a different ending (*B. patellaris*). DARWIN (1854) also missed BRUGUIÈRE's paper and used GMELIN's name, as did subsequent authors up through NEWMAN and ROSS (1976). However, as noted by HENRY and McLAUGHLIN (1975), LAMY and ANDRÉ (1932) had recognized BRUGUIÈRE's priority and in accordance with the Principal of Priority outlined in the International Code of Zoological Nomenclature, this author and his spelling of the name are also used here.

Diagnosis

Shell surface smooth in juveniles, ribbed in old specimens, conical to cylindrical, the circumference is pentagonal or quadrangular respectively. Radii narrow to wide, summits rough, disparietal. Sheath with calcareous vesicles. Parietal tubes often subdivided into several rows of subsidiary tubes; no transverse septum in the lower part. Scutum usually flat, sometimes externally concave; adductor ridge short to moderately long. Tergum with carinal margin convex and prominent; with spur furrow open; basal margin on scutal and carinal sides usually straight; spur width approximately 0.4 length of basal margin; distance between basiscutal angle and anterior side of spur nearly 0.6 of spur width. Labrum with 3–5 teeth on either side of the notch. Cirrus II with simple spinules; without conical teeth on outer face near anterior margin. Cirrus III without complex setae; with conical teeth on anterior margin of anterior ramus.

Description

Shell (Figs 1A–D) conic to cylindrical, sometimes depressed, the circumference pentagonal or quadrangular. Color of parietes externally dirty white, bluish white or violet brown; in old specimens dirty brown with longitudinal bands, and whole surface finely ribbed to the basis; in young specimens are regularly banded longitudinally, with dirty white and violet brown. Shell internally white, sheath purplish; growth ridges fringed with brown membrane. Orifice moderately oval to rhomboidal. Width of shell more than 1/2 carino-rostral diameter; surface with longitudinal folds. Radii narrow in conic specimens, usually moderately wide in cylindrical specimens, horizontally striate; summits dispariental, beveled, arched or rounded; sutural edges bluntly, moderately denticulate on lower margins; color of radii dirty white or dull red often with brown band ribbed parallel to basis; in young specimens externally quite smooth. Alae with summits transparietal (nearly parallel to the base); sutural edges septate, finely crenate; dirty brown with raised margin of same color as parietes. Sheath vesicular (cavity between sheath and inner lamina has calcareous vesicles). Inner lamina ribbed below, often extending to sheath, denticulate basely. Parietal tubes with transverse septa at 1/2–1/3 their length, each of the longitudinal tubes is accompanied by small (subsidiary) tubes. They are formed by secondary longitudinal septum which pro-

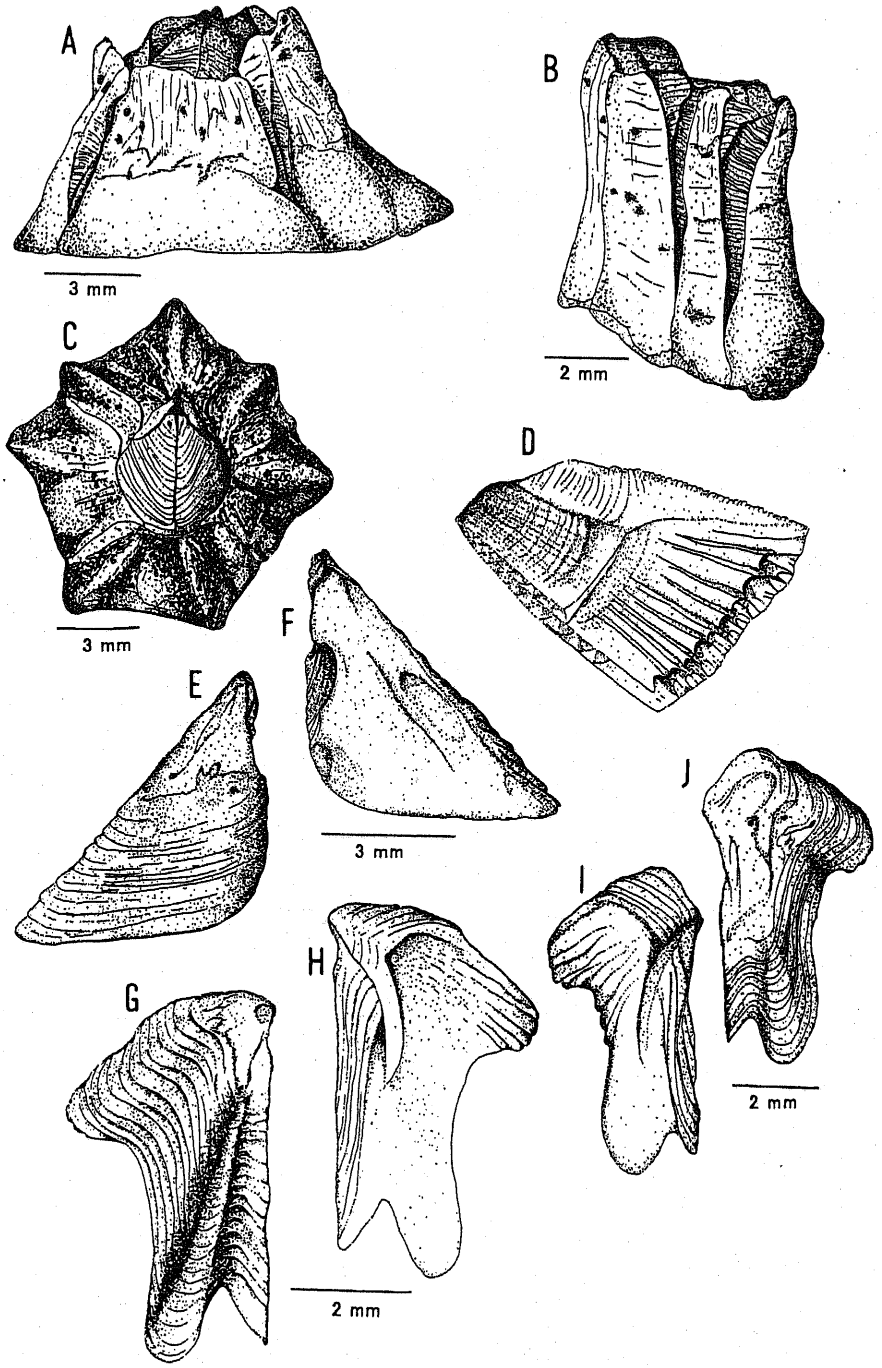

Fig. 1. *Balanus patelliformis* BRUGUIÈRE, shell features. (A) conical specimen, rostral view (13-ST); (B) tubular specimen, lateral view (15-ST); (C) pentagonal specimen, apical view (09-ST); (D) schematic view of shell structure (13-ST); (E) scutum, outer surface (01-ST); (F) scutum, inner surface (01-ST); (G, I) terga, outer surface (G: 01-ST and I: 12-ST, respectively); (H, J) tergum, inner surface (H: 01-ST and J: 12-ST, respectively).

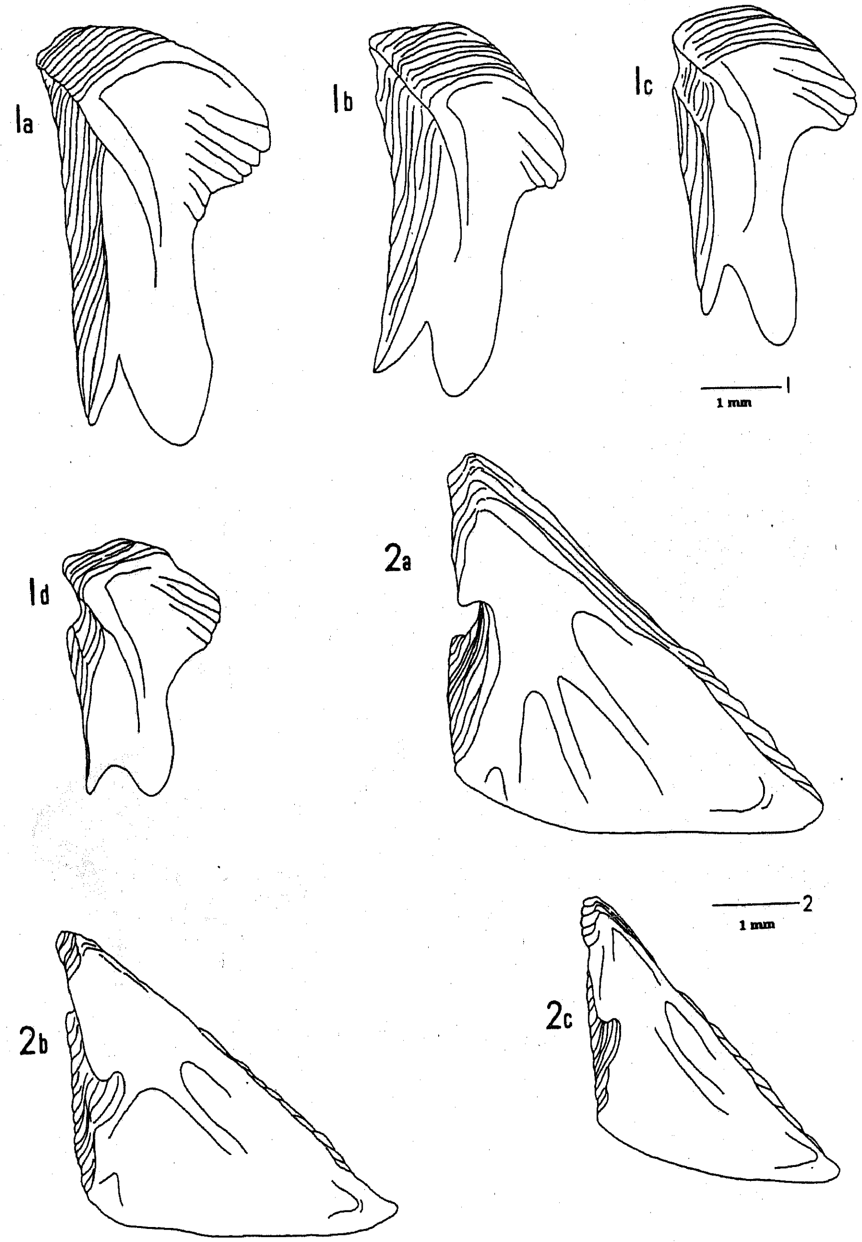

Fig. 2. The morphological variation of inner surfaces of terga and scuta of *B. patelliformis* BRUGUIÈRE. (1) terga: (1a) 03-ST; (1b) 20-ST; (1c) 18-ST; (1d) 21-ST, (2) scuta: (2a) 19-ST; (2b)02-ST; (2c) 04-ST.

ject from the outer lamina and joint to the wall of the primary longitudinal septum. Basis thin, calcareous, with radial tubes extending nearly to periphery.

Opercular plates (Figs 1E–J; 2, 1a–d, 2a–c). Scutum with outer surface flat, apex sometimes recurved with respect to exterior; tergal margin straight unless notched by corrosion; occludent margin moderately toothed; growth ridges low to moderate, but in old specimens upper part moderately folded; usually longitudinal striae absent. Inner surface smooth, occasionally roughened near apex; articular ridge prominent, slightly reflexed at about half length of tergal

Table 1. Qualitative comparison of characters of *B. patelliformis*, *B. kondakovi*, *B. albicostatus*, and *B. improvisus*.

Characters	*B. patelliformis*	*B. kondakovi*[1)]	*B. albicostatus*[2)]	*B. improvisus*[3)]
A. **Shell**				
1. Shape	conical to cylindrical	subcylindrical to cylindrical	conical to cylindrical	conical
2. Parietes	smooth, ribbed, folded with longitudinal ribs	smooth without longitudinal ribs	ribbed with longitudinal ribs	very smooth without longitudinal ribs
3. Parietal tubes	with transverse septa	with transverse septa	with transverse septa	with transverse septa
4. Subsidiary tubes	present	sometimes present	present	sometimes present
5. Sheath	vesicular	vesicular	vesiculer	solid
6. Radii	narrow	narrow	wide	narrow
7. Alae	transparietal	disparietal	dispariental	disparietal
B. **Scutum**				
8. Adductor ridge	short	short	short	moderately long
C. **Tergum**				
9. Spur furrow	open	open	closed	open
10. Crest of depressor muscle	very prominent	moderately prominent	very prominent	very prominent
11. Basal margin of carinal side	straight or slighly concave	excavated, often deeply	slightly concave	straight or slighly concave
D. **Mouth-parts**				
12. Labrum	simple	simple	simple	multidenticulate
13. Maxilla I	with notch[4)]	with notch	with notch	without notch
E. **Cirrus III**				
14. Anterior margin	with conical teeth	with conical teeth	without conical teeth	with conical teeth
15. Erect tooth on posterodistal angles of articles	absent	absent	absent	absent
16. Setae	with complex setae[5)]	with complex	with complex setae	without complex setae
F. **Basidorsal point of penis**	naked	with 2 apical setae	naked	naked, very low

[1, 2, 3)] *B. kondakovi* and *B albicostatus* from Oikebajomae, Tokyo Bay; *B. improvisus* from Sendai (I.A. Puspasari, original data); [4)] without notch (Fernando, 1978); [5)] with complex setae (Fernando, 1978).

margin (Tables 1, 2), and bluntly or sharply pointed; articular furrow deep; adductor ridge usually moderately long, sometimes short, well separated from articular ridge; sometimes with narrow, shallow pit on lower tergal side; lateral depressor muscle pit small, usually very shallow but sometimes wanting. Color of scutum externally usually brownish purple, occasionally dirty white; internally white with splotches of purple. Tergum with articular margin raised, sometimes denticulate at lower margin; carinal margin convex, sometimes protuberant in upper third; growth ridges are moderate, usually crenulate; basal margin usually straight on both sides of spur, sometimes slightly concave on carinal side; spur furrow open and broadly rounded at end; spur width approximately 0.39 length of basal margin; distance between basiscutal angle and spur nearly 0.55 of spur width (Table 2). Internally, articular ridge moderately prominent, reflexed at apex; articular furrow deep; crest for depressor muscles prominent with numerous (5–8) insertion sites, usually projecting below basal margin; sometimes surface rugose in upper part, and basely smooth. Color of tergum externally mostly purplish-pink or brownish purple, with white spur furrow open; internally purple, but usually white on spur, articular ridge, crest of depressor muscle, and carinal segment.

Mouthparts. Labrum (Fig. 3B) usually with 3–5 (mean = 4.23) teeth and with five setules on each crest of notch. Palps with short, pinnate setae in narrow band near upper margin, with long setae on lower half of distal margin and in an oblique row near distal angle. Mandible (Figs. 3C, D, E) with 4–5 teeth, 3rd–5th teeth sometimes bifid, with are additional small

Table 2. Meristic comparison of characters of opercular plates, trophi and cirri of *B. patelliformis*, *B. kondakovi*, *B. albicostatus*, and *B. improvisus*.

Parameters	*B. patelliformis* (n=23)		*B. kondakovi*[1] (n=6)		*B. albicostatus*[2] (n=12)		*B. improvisus*[3] (n=93)	
	Range	x	Range	x	Range	x	Range	x
A. **Tergum**								
1. Spur width/basal margin	0.31–0.59	0.39	0.26–0.33	0.30	0.32–0.44	0.36	0.12–0.36	0.36
2. Spur length/spur width	0.59–0.94	0.77	1.21–1.67	1.37	0.52–0.83	0.65	0.73–2.44	1.59
3. Distance from angle/spur width	0.31–0.81	0.55	1.25–1.78	1.57	0.33–0.47	0.42	0.29–1.80	0.87
4. Distance from angle[4]/spur length	0.46–1.05	0.63	1.00–1.38	1.20	0.50–0.80	0.65	0.27–0.91	0.54
5. Distal from angle/basal margin	0.13–0.34	0.22	0.38–0.56	0.46	0.12–0.18	0.15	0.09–0.25	0.17
6. Spur length/basal margin	0.25–0.35	0.30	0.35–0.45	0.40	0.18–0.28	0.23	0.24–0.47	0.32
B. **Scutum**								
7. Articular ridge/tergal margin	0.43–0.65	0.53	0.74–0.98	0.86	0.35–0.57	0.47	0.60–0.89	0.74
8. Articular ridge/occludent margin	0.28–0.42	0.37	0.30–0.36	0.33	0.18–0.25	0.22	0.33–0.56	0.45
C. **Trophi**								
9. Number of teeth on labrum (each side of notch)	3–5	4.23	4–5	4.33	2–3	2.92	7.5–21.5	15.11
D. **Cirri**								
10. Number of paired setae per segment, cirrus VI	4–6	4.78	4–6	5.00	4–6	5.25	5–8	6.09
11. Ratio of the length of the longest of medial article of cirrus III to the width of its article[5]	1.28–1.63	1.41	1.43–1.88	1.63	1.27–1.48	1.34	1.97–2.45	2.21

[1], [2] *B. kondakovi* and *B. albicostatus* from Oikebajomae, Tokyo Bay (I.A. PUSPASARI, original data).

[3] *B. improvisus*, locality unstated (HENRY and MCLAUGHLIN, 1975 : 206).

[4] Point farthest from basicutal angle on proximal half of scutal margin of spur.

[5] SOUTHWARD and NEWMAN, 1998.

teeth in between 1st–2nd or 2nd – 3rd; with inferior angle spinose; 5th tooth confluent with inferior angle. First maxilla (Fig. 3A) with small notch, including 2 or 3 fine spines, below upper pair of spines; 6–8 (mean= 6.41) spines between notch, and the last pair of spines occupying inferior angle. Second maxilla bilobed with long setae on outer margin of distal lobe, and pinnate setae near lower margins of both lobes.

Cirri. Protopods of anterior cirri primarily with pinnate setae, sometimes with plumose setae; protopods of cirrus I with simple spinules below posterodistal angle; basopodite of cirrus I sometimes with narrow band of simple spinules below distal articulations; basopods of cirri II and III with narrow band of simple spinules below distal articulations. Number of articles in each right cirrus of *B patelliformis* are listed in Table 3.

Cirrus I with anterior ramus 4–10 (mean=7.1) articles longer than posterior ramus; articles of both rami, especially the posterior one, strongly protuberant and with well developed simple spinules on anterior margins and inner faces of both rami; with long setae extending along sutures of posterodistal and anterodistal angles of outer face, also with multifid spinules near posterior margins of distal articles; several proximal articles each with narrow band of simple scales on outer face.

Cirrus II with anterior ramus equal to or 1–2 (mean=1.2) articles longer than posterior; both rami with moderately protuberant articles; distal articulations with long setae, and multifid spinules near anterior and posterior margins of medial and proximal articles; few proximal articles of each ramus with narrow band of spinulose scales on outer face near posterior margin.

Cirrus III (Figs 3F–H) with anterior ramus 1–5

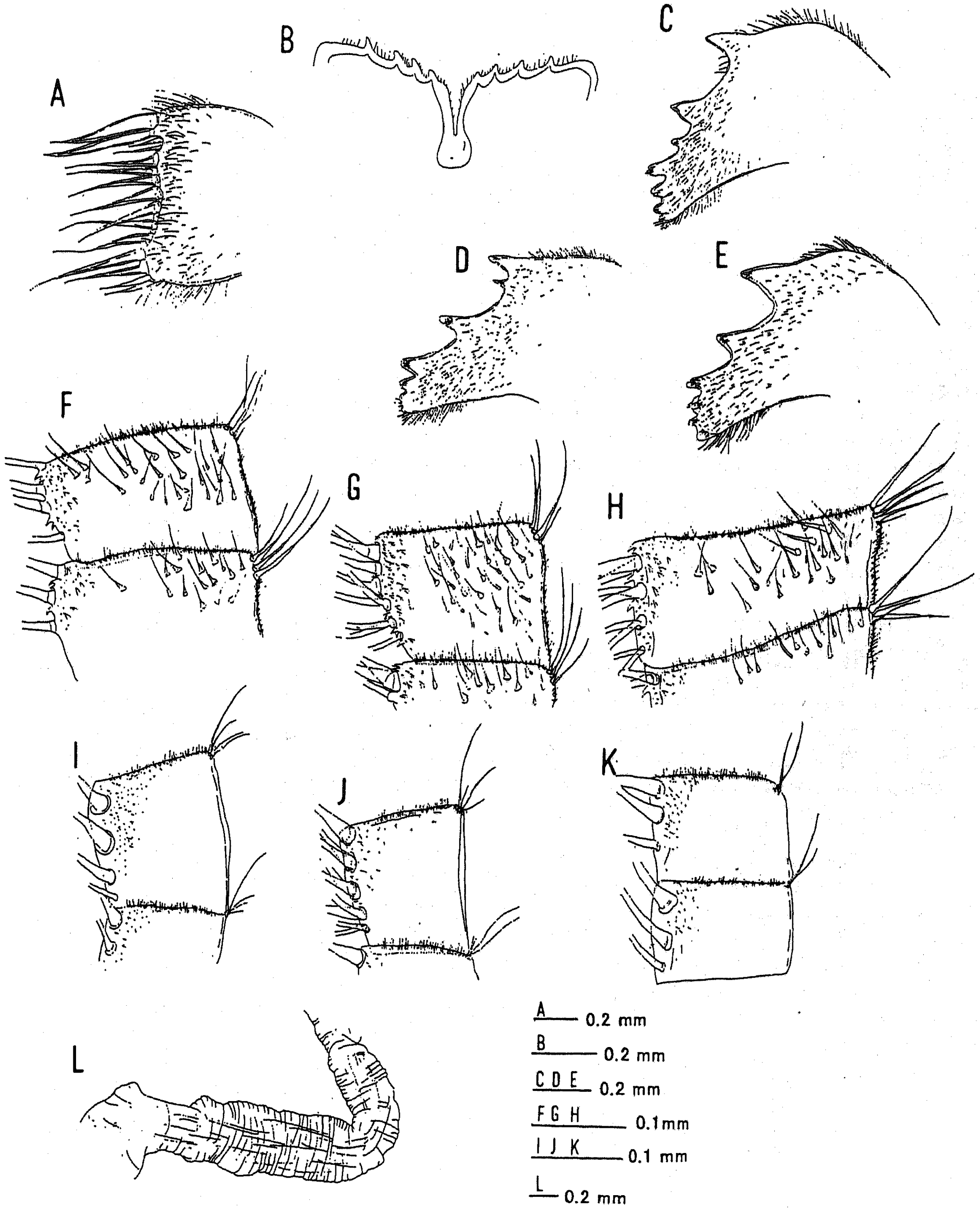

Fig. 3. *Balanus patelliformis* BRUGUIÈRE, trophi and cirri. (A) first maxilla (10-ST); labrum (07-ST); (C, D, E) mandible (C: 12-ST), (D: 13-ST), (E: 18-ST); (F–H), anterior ramus of left cirrus III (13-ST), (F) proximal, (G) medial, and (H) distal segments; (I–K), anterior ramus of left cirrus IV (13-ST), (I) proximal, (J) medial and (K) distal segments; (L) basal part of penis (08-ST).

Table 3. Number of articles in each right cirrus of *B. patelliformis*.

Specimen number	Number of articles of cirri											
	I		II		III		IV		V		VI	
	a	p	a	p	a	p	a	p	a	p	a	p
01-ST	24	15	19	17	18	17	29	31	38	34	37	34
02-ST	24	14	17	17	20	17	20	31	36	33	36	33
03-ST	25	12	16	16	17	16	33	31	34	35	36	32
04-ST	21	12	15	15	18	16	27	27	28	29	27	28
05-ST	21	12	16	16	21	19	30	31	36	34	39	37
06-ST	21	16	16	14	—	—	29	31	34	31	38	37
07-ST	19	11	16	16	20	15	29	32	34	33	35	32
08-ST	19	14	15	17	18	14	28	31	36	32	36	34
09-ST	21	14	17	20	20	19	30	31	42	36	40	37
10-ST	17	13	15	14	18	15	29	28	34	35	40	38
11-ST	21	16	16	15	17	15	33	31	42	35	43	39
12-ST	—	—	16	12	17	14	28	30	—	—	35	32
13-ST	20	16	17	16	20	18	30	28	36	32	39	37
14-ST	19	15	15	14	21	17	28	29	29	32	36	34
15-ST	21	13	13	12	18	15	27	26	33	29	—	—
16-ST	17	12	16	15	18	17	27	29	35	34	38	37
17-ST	18	12	16	12	15	17	31	33	34	35	40	39
18-ST	17	13	20	12	16	14	32	33	38	39	45	39
19-ST	20	14	15	15	18	17	27	29	35	38	40	46
20-ST	19	12	16	15	19	15	30	29	31	34	37	38
21-ST	18	10	15	14	20	18	29	28	33	34	36	39
22-ST	19	14	17	15	21	17	33	31	34	32	39	41
23-ST	23	16	19	16	18	16	30	32	36	34	37	35
N	22	21	23	23	22	22	23	23	22	22	22	22
x	20.2	13.1	16.2	15.0	18.6	16.2	29.5	30.1	34.9	33.7	37.4	36.3

N: number of individuals examined.
x: arithmetic mean; a: anterior, p: posterior.

(mean = 2.5) articles longer than posterior; both rami with slightly protuberant articles; distal articles with moderately long setae and spinules; posterior margin of distal angel with simple spinules below relatively long setae; inner faces occasionally with subarticulation row of simple spinules and a lot of setae. Anterior margins on anterior ramus with conical teeth on proximal, medial, and distal articles; posterior ramus without teeth. Outer surface near anterior margins of both rami with long proximal articles and narrow band of simple scales, with 4–6 pairs of moderately long setae, and simple spinules near distal angles. Posterior margin with 5 or 6 relatively long setae on distal angles of most articles. Outer surface near posterior margin of long proximal articles of anterior ramus with narrow to wide band of simple scales. Inner surface near posterior margin of proximal articles of anterior ramus, with narrow band of simple spinules and a few of long setae. Posterior cirri with well-developed multifid spinules near anterior margins and narrow band of simple spinules on inner surface near posterior margin; on distal articulation with a numerous short setae and 3–5 longer setae on each posterodistal angles.

Anterior ramus of cirrus IV (Figs 3I–K) with simple spinules; without conical teeth on outer surface near anterior margin of articles, occasionally also lacking them on all distal articles; with band of well-developed denticles down anterior margin of outer surface, and multifid spinules below distal articulation. Cirri V and VI usually with 1 or 2 simple spinules below setae on each proximal article, sometimes also on each median articles. Cirrus VI with 4–6 (mean = 4.8) pairs of setae on anterior margin of each median article.

Basidorsal point of penis narrow, usually elongate, naked (Fig. 3L).

Size

The diameter of DARWIN's (1854) specimen was 23 mm (Pl. 6, Figs 5a–5c); the Greatest diameter of NILSSON-CANTELL's (1929) specimen was 18 mm, height 7 mm (Fig. 1). The specimens in the present study, all within this range (Appendix). The rostro-carinal diameter of the largest specimen 19-ST was 19.8 mm, the carino-lateral diameter 21 mm, and the height 11 mm. The largest carino-lateral diameter of specimen 01-ST was 28.5 mm with a rostro-carinal diameter 17.3 mm, and height 9.2 mm. The highest specimen 23-ST was 11.5 mm with a rostro-carinal diameter 13.6 mm, and a carino-lateral diameter 10.8 mm.

Variation

The shell varies in shape and surface relief; crowded specimens maybe cylindrical or quadrangular with a wide orifice and radii, usually with the surface ribbed or folded; in less crowded individuals, shells become conical or depressed, pentagonal with narrow radii, and often with a smooth surface. The carinal side of the basal margin of the tergum is also variable, usually broadly excaved but sometimes looking hollowed out due to an extension of the crest area for the tergal depressor muscles.

Habitat

Balanus patelliformis was found in abundance associated with *B. amphitrite* and *Chthamalus* sp., attached to the leaves and stems of *Avicenia alba*, *Rhizophora mucronata*, and *Sonneratia caseolaris* seedlings planted on a new mudflat. The seedlings, planted at high, mid, and low-tidal levels, experienced salinity ranging from 0‰–28‰ (ANGSUPANICH and HOVANONA, 1996). According to UTINOMI (1968), *B. patelliformis* occurs in the Malacca Strait from the intertidal zone to 40 m of depth, attached on living or dead sunken "bark of a palm-trees" or wood, shell, often with *B. variegatus* or *C. malayensis*.

Discussion

Material collected from Ban Don Bay, Surat Thani, Thailand, agrees with the hard parts described by DARWIN (1854) and UTINOMI (1968), the hard parts and appendages described by NILSSON-CANTELL (1921, 1929, 1938) and HENRY and McLAUGHLIN (1975).

Balanus patelliformis had been collected from Coromandel and the Malabar coast (SPENGLER, 1780); the south coast of India (BRUGUIÈRE, 1792); the Porto Novo Region, southern India (PATEL, pers. com., FERNANDO, 1978); Bengal and the Philippine archipelago (DARWIN, 1854); Nordwachter, Javasee (i.e. Java Sea) (NILSSON-CANTELL, 1921); Rangoon (NILSSON-CANTELL, 1929); the Orissa and Arakan coasts of the Bay of Bengal (NILSSON-CANTELL, 1938), and the Strait of Malacca (UTINOMI, 1968). Therefore, this species is apparently limited to the Indian Ocean and the Malay and Philippine archipelago, as shown in fig. 4.

DARWIN's material (1854, Pl. 6, Figs 5a–5c) from Bengal and the Philippine archipelago exhibits a depressed shell form, sometimes much depressed. Usually the surface of the shell is smooth, but in older specimens the wall is slightly folded longitudinally. The tergum has a straight basal margin and the basis lacks radial tubes. NILSSON-CANTELL's material (1921: 328; 1929: 4, Figs 1a–b, 3a–b; 1938: 46, Pl. 1, Figs 4, 5) from Nordwachter Java Sea, Rangoon, Orissa, and the Arakan coast has conical, with strongly but regularly, folded walls. The basal margin of tergum is deeply excavated on the carinal side as in *B. kondakovi*, and the basis had subsidiary tubes. UTINOMI's (1968: 174, Figs 5, 6a, b) material from the Strait of Malacca usually has a columno-conical or depressed-conical wall with smooth parietes; the basal margin of the tergum is broadly excavated on the carinal side, and the basis has subsidiary tubes. In our specimens from Ban Don Bay, the shape and surface texture of the shell, the basal margin of the tergum, and the armature of the mandible are rather variable. The shell shape ranges from conical to cylindrical with the surface folded or ribbed, but sometimes the shell is depressed with the surface often smooth. When crowded, the shells become cylindrical and tall, but in less crowded condition they tend towards conical, although the carina is often close to vertical. The carinal side of the basal margin of the tergum is also quite variable, usually straight, sometimes slightly concave, but no specimens is as deeply excaved as figured by NILSSON-CANTELL (1929). The mandible usually has five teeth, sometimes has an additional small tooth between the 1st and 2nd or 2nd and 3rd teeth, and these characters are similar to those of NILSSON-CANTELL's (1929) specimens.

In material of *B. patelliformis* from Porto Novo, South India, by FERNANDO (1978) found cirrus III

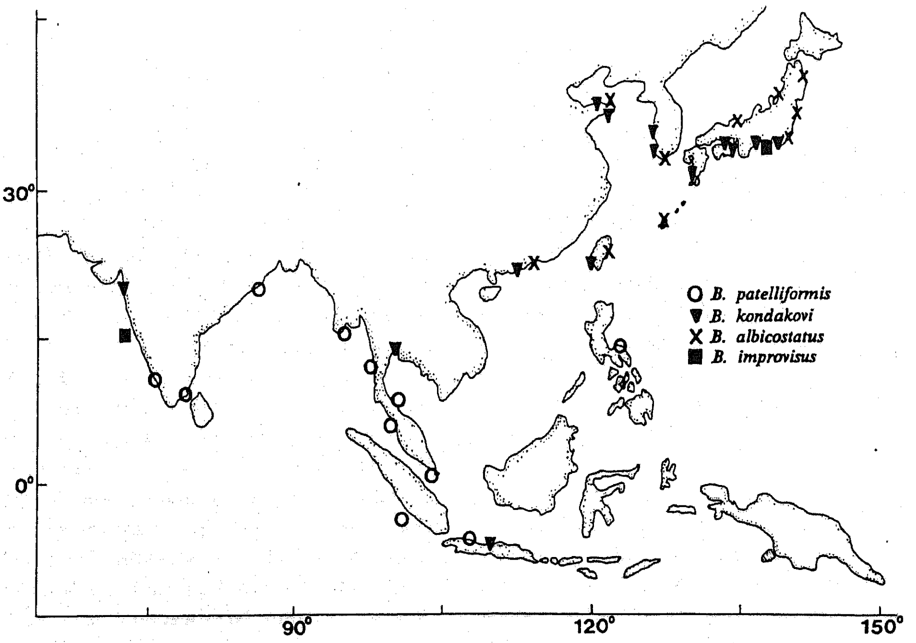

Fig. 4. Geographical distribution of *B. patelliformis*, *B. kondakovi*, *B. albicostatus*, and *B. improvisus* (compiled from NISSON-CANTELL, 1921, 1929, 1938; UTINOMI, 1968; HENRY, 1973; HENRY and MCLAUGHLIN, 1975; YAMAGUCHI, 1977a, 1977b, 1980; LEWIS, 1985).

armed with complex setae and the first maxilla without a notch. Many of the specimens in our material have a notch on the first maxilla as described by HENRY and MCLAUGHLIN (1975), but usually no complex setae on cirrus III. Some of the morphological characters of our specimens differ from those described by HENRY and MCLAUGHLIN (1975: 142, Pl. 16, Pl. 17, Figs f–j): 1) in the present of transverse septa in the parietal tubes; 2) a longer articular ridge on the scutum; and 3) a greater relative width of the tergal spur.

Affinities

DARWIN (1854) placed *B. patelliformis* in his section D of the genus *Balanus* based on diagnostic external shell characteristics: 1) basis without pores, 2) the color of shell surface. However, DARWIN (1854 : 261) remarked that this species has a strong claim to be ranked in his section C because the basis sometimes has subsidiary tubes near periphery and the species this appeared to DARWIN to be more closely related to *B. improvisus* than to any other species of *Balanus*. On the other hand, HENRY and MCLAUGHLIN (1975: 144) suggested that several characters, particularly those of the labrum and tergum, the shell surface, and the cirri give further evidence for a close relationship of *B. patelliformis* with the subsequently described species *B. kondakovi* and *B. albicostatus* respectively (TARASOV and ZEVINA, 1957; PILSBRY, 1916). As previously mentioned, the figure of the tergum of *B. patelliformis* (NILSON-CANTELL, 1929: Fig. 1a) is very similar to *B. kondakovi* in the deep excavation on the scutal side of the spur and the denticulate basal margin on the carinal side.

Morphological differences between *B. patelliformis*, *B. kondakovi*, *B. albicostatus*, and *B. improvisus* are listed in Tables 1 and 2. The lacks of the multidenticulate labrum and solid sheath separates *B. patelliformis* from *B. improvisus*. *B. patelliformis* appears to lie between *B. kondakovi* and *B. albicostatus*. Some characters (shell, spur, mouthparts, basidorsal point) ally it more closely with *B. albicostatus*, and the other character of anterior margin of cirrus III resembles to *B. kondakovi*. On the other hand, characteristics of the radii, alae, the longitudinal striae of scutum, and cirrus III do not show a close affinity with *B. albicostatus*, and also can be differentiated from *B. konda-*

kovi by several characteristics of alae, basal margin of tergum, and complex setae of cirrus III. The radii of uncrowded *B. patelliformis* are narrow, which it similar to *B. kondakovi*, whereas those of *B. albicostatus* are moderately to very wide. The longitudinal striae of scutum are usually absent in adult of *B. patelliformis* like as *B. kondakovi*, but in young specimens almost present, while in *B. albicostatus* fine striae are present in young and adult specimens. The anterior margin of cirrus III of *B. patelliformis* are similar to *B. kondakovi*, as has conic teeth, whereas *B. albicostatus* lack conical teeth.

Geographical distribution

The geographical distribution of *B. patelliformis*, *B. kondakovi*, *B. albicostatus*, and *B. improvisus*, compiled mainly from NILSSON-CANTELL (1921, 1929, 1938), HENRY (1973) , HENRY and MCLAUGLIN (1975), YAMAGUCHI (1977a, 1977b, 1980), and LEWIS (1985) is given in figure 4. As can be seen, *B. kondakovi* has a wide range in the Indo-West Pacific, from Bombay through the Java Sea to south-western Korea and southern Japan. The record for *B. kondakovi* on the west coast of India (LEWIS, 1985), while certainly possible, could actually be for young or crowded *B. patelliformis*. *Balanus albicostatus* on the other hand, is only found in the Western Pacific Ocean, from Japan, North China through Korea, Hong Kong and Formosa. HENRY & MCLAUGLIN (1975) reported *B. albicostatus* from Morro Bay, California, but it apparently didn't become established there. *B. improvisus* DARWIN, 1854, presently ranges widely in tropical and warm temperate seas (Scotland and the Baltic Sea to West Africa, Mediterranean, Black, Caspian, and Red Seas; Nova Scotia to Patagonia; Oregon to Peru; Japan, Strait of Malacca, and Australia), but it was apparently introduced to the Indo Pacific by ships.

Summary

B. patelliformis is, in general, found attached to the leaves and stems of marine vascular plants or shells in the intertidal zone to 40 min depth, and it can tolerate wide variations in salinity. The phylogenetic relationship of *B. patelliformis* appears to be between *B. kondakovi* and *B. albicostatus*. More precise determination of their will requires other methods such as cladistic analysis, allozyme gel electrophoresis, and/ or mt DNA sequencing.

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Registered numbers of specimens examined are listed below. They are deposited in the National Science Museum, Tokyo (NSMT).

NSMT-Cr 13038 for 01-ST in this text
NSMT-Cr 13039 for 02-ST
NSMT-Cr 13040 for 03-ST
NSMT-Cr 13041 for 04-ST
NSMT-Cr 13042 for 05-ST
NSMT-Cr 13043 for 06-ST
NSMT-Cr 13044 for 07-ST
NSMT-Cr 13045 for 08-ST
NSMT-Cr 13046 for 09-ST
NSMT-Cr 13047 for 10-ST
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NSMT-Cr 13049 for 12-ST
NSMT-Cr 13050 for 13-ST
NSMT-Cr 13051 for 14-ST
NSMT-Cr 13052 for 15-ST
NSMT-Cr 13053 for 16-ST
NSMT-Cr 13054 for 17-ST
NSMT-Cr 13055 for 18-ST
NSMT-Cr 13056 for 19-ST
NSMT-Cr 13057 for 20-ST
NSMT-Cr 13058 for 21-ST
NSMT-Cr 13059 for 22-ST
NSMT-Cr 13060 for 23-ST

Appendix

Measurements of shell walls, opercular plates (in mm), number of spines and/or teeth of trophi, and of paired setae of cirrus VI of *B. patelliformis*.

Specimen number	rostro-carinal diameter at base	carino-lateral diameter at base	height	length of basal margin of tergum	spur length	spur width	distance from basicutal angle to margin of spur	length of articular margin of scutum	length of articular ridge of scutum	length of occudent margin of scutum	number of teeth on right side of labrum	number of teeth on left side of labrum	paired spines between the upper and lower first maxilla	teeth of the mandible	paired setae per segment of left cirrus VI
01-ST cy	17.3	28.5	9.2	0.8	9.9	0.32	0.21	0.89	0.38	1.34	–	–	6	5	5
02-ST co	17.3	14.5	7.8	0.8	8.8	0.32	0.26	0.87	0.47	1.18	–	–	–	–	–
03-ST co	16.9	14.7	7.7	0.9	8.7	0.37	0.18	0.78	0.45	1.32	4	5	6	5	4
04-ST co	13.9	7.3	5	0.6	7.1	0.25	0.18	0.84	0.49	1.38	4	5	7	5	5
05-ST co	19.3	17.4	6.8	0.8	8.5	0.3	0.18	1.31	0.58	1.49	5	5	7	5	4
06-ST co	17.2	15.5	5.8	0.9	8.8	0.37	0.19	0.88	0.5	1.37	5	4	6	5	4
07-ST co	9.2	4.8	3.3	0.5	3.9	0.19	0.15	0.8	0.4	1.05	5	5	6	5	5
08-ST co	18	14.5	7.8	0.8	8.1	0.32	0.19	0.92	0.53	1.19	3	5	7	5	6
09-ST co	16.9	16.7	4.2	0.8	8.1	0.28	0.23	0.83	0.46	1.31	4	5	7	5	5
10-ST co	15.2	10.5	5.3	0.7	7.7	0.25	0.13	0.81	0.43	1.41	5	4	7	5	5
11-ST cy	13.9	13.1	8	0.7	8.5	0.27	0.2	0.79	0.45	1.3	5	4	8	5	5
12-ST co	13.7	13.5	8.1	0.7	8.3	0.3	0.1	0.86	0.52	1.31	5	4	6	6	5
13-ST co	12.4	12.2	6.1	0.6	6.8	0.21	0.11	0.98	0.45	1.14	5	5	6	5	4
14-ST co	12.8	11.6	6.2	0.6	8.7	0.24	0.17	0.95	0.45	1.38	3	5	8	5	5
15-ST cy	9.6	10.3	10.2	0.7	9.8	0.22	0.15	0.95	0.43	1.22	4	3	6	5	5
16-ST co	17.4	16.6	7.1	0.8	9.9	0.31	0.14	0.74	0.41	1.16	3	5	7	5	5
17-ST co	16	19.7	7.4	–	12.5	–	–	–	–		4	4	6	5	4
18-ST cy	11	9.1	8	0.6	7.9	0.2	0.15	0.89	0.42	1.22	5	5	–	5	5
19-ST co	19.8	21	11	0.8	11.7	0.24	0.14	1.01	0.51	1.51	5	4	7	5	5
20-ST cy	11.2	9.5	8.3	0.6	8.4	0.36	0.13	0.83	0.42	1.04	4	3	8	5	4
21-ST co	10.2	11.2	8.3	0.4	7.4	0.14	0.06	0.51	0.32	0.91	3	5	–	5	5
22-ST cy	11.9	10.8	8.3	0.9	7.8	0.35	0.24	0.79	0.51	1.24	5	4	6	5	4
23-ST cy	13.6	10.8	8.3	0.9	9.7	0.35	0.11	0.44	0.55	1.32	5	3	7	5	5

Abbrevations : cy, cylindrical; co, conical

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Phylogeny of the *Balanus amphitrite* complex occurring in Japan (Cirripedia: Balanidae) inferred from mitochondrial COI gene nucleotide sequences and morphology

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Abstract

The phylogeny of the six species of the *Balanus amphitrite* complex found in Japan was analyzed based on nucleotide sequences of the mitochondrial COI (cytochrome oxidase subunit I) gene and the morphology of the barnacles. The six species are *B. amphitrite* Darwin, *B. eburneus* Gould, *B. improvisus* Darwin, *B. albicostatus* Pilsbry, *B. kondakovi* Tarasov and Zevina, and *B. reticulatus* Utinomi. Judging from the high bootstrap values in the sequence-based phylogeny, these six species appear to comprise a monophyletic group divided into two clusters of three species each: *B. amphitrite*, *B. eburneus*, and *B. improvisus*; and *B. albicostatus*, *B. kondakovi*, and *B. reticulatus*. The cladogram based on morphology is congruent with the sequence-based one; the first species cluster is characterized by a multidenticulate labrum, the second by a simple labrum.

Key words: *Balanus amphitrite* complex, morphology, cladistic analysis, molecular phylogeny, Japan

Introduction

The group of barnacles comprising the *Balanus amphitrite* complex is species rich, with worldwide distributions for some species in warm temperate and tropical waters due to dispersal by ships. Newman (1993) summarized the history of the systematics of the nine varieties of *B. amphitrite* originally described by Darwin (1854) (Fig. 1). Because of Darwin's short descriptions and lack of complete collecting data, type localities are dubious, and type-specimens largely undesignated; therefore, much confusion has ensued in the subsequent literature. Utinomi (1967) described six species of the *B. amphitrite* complex from Japan: *B. reticulatus* Utinomi, 1967, *B. variegatus cirratus* Darwin, 1854, *B. albicostatus* Pilsbry, 1916, *B. amphitrite* Darwin, 1854, *B. amphitrite formosanus* Hiro, 1938, and *B. uliginosus* Utinomi, 1967 (=*B. kondakovi* Tarasov and Zevina, 1957) (Fig. 1). A seventh species, *Balanus poecilotheca*, had been described by Krüger (1911) from Okinose Bank, Sagami Bay. Writing under his former name of Hiro (1938), Utinomi once placed *B. poecilotheca* in the *B. amphitrite* complex, but he later excluded this species from the complex (Utinomi, 1967).

Hiro (1938) reported *B. amphitrite* forma *cirratus* Darwin from Iki Island and Ariake Bay, Kyushu. However, based on an examination of Darwin's collection kept at the British Museum (Natural History), Harding (1962) replaced this scientific name with *B. variegatus* var. *variegatus*. Utinomi (1967) called the specimens from Iki Island and Ariake Bay *B. variegatus cirratus*. Since then, this species has been hard to find in the waters of Japan (Yamaguchi, pers. observ.), and it is not

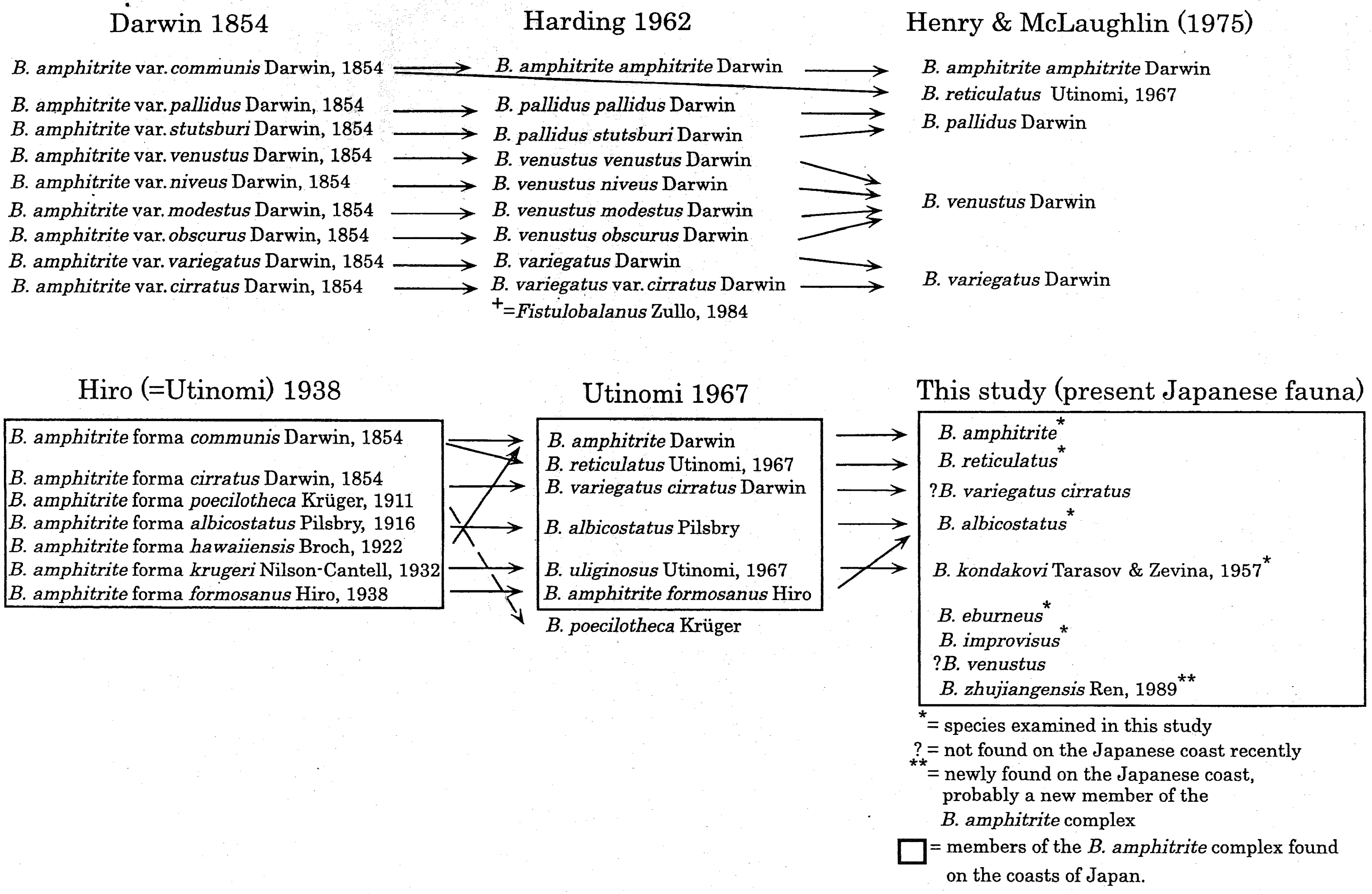

Fig. 1. Historical changes of taxonomy of some species of the *Balanus amphitrite* complex including Darwin's (1854) nine varieties and species found today on the coasts of Japan (Upper: after Yamaguchi, 1977; Newman, 1993).

included in the present study.

Utinomi (1970) reported *B. venustus venustus* Darwin,1854 from Aikawa, Sado Island, Niigata Prefecture, and also from Otomi in Uchiura Bay, Fukui Prefecture. After that, there has been no other report on the occurrence of this species or subspecies in Japan.

There has been a dramatic change in the species composition of the intertidal barnacle fauna in Tanabe Bay, Osaka Bay, Tokyo Bay, and other bays of Honshu, Japan, over the last 15 years (Yamaguchi, unpublished data). In particular, *B. reticulatus* has either decreased in, or been excluded from, the lower intertidal zone of embayments in Japan. Concomitant with the decrease in number of individuals or complete disappearance of this species in some places, the vertical distribution of *B. amphitrite* and *B. albicostatus* has shifted from the middle to the low intertidal zone. Furthermore, the numbers of individuals of *B. amphitrite* and *B. albicostatus* have also decreased (Yamaguchi, unpublished data).

In the 1970s *B. reticulatus* was common in various embayments in Japan, but now it is not easily found. The specimens of *B. reticulatus* examined in our study were collected from the open shore of Okinawa Island. *Balanus amphitrite* appears to have arrived on the Japanese coasts in historical times, as assumed by Hiro (1938) and corroborated by Yamaguchi (1977) based on the fossil record. *Balanus eburneus* Gould, 1814 and *B. improvisus* Darwin, 1854 arrived in Japanese waters even more recently, after World War II (Kawahara, 1963), and Yamaguchi (1989) showed the geographic distribution of both species in Japan. *Balanus amphitrite, B. albicostatus, B. eburneus,* and *B. improvisus* are widely distributed throughout Japan in embayments, except in Hokkaido in northern Japan. They are fouling organisms and get about through human agency, for example on the hulls of ships.

Henry and McLaughlin (1975) attempted a qualitative and quantitative study of the recent taxa of the *B. amphitrite* complex. The complex included 19 species and 4 subspecies, namely, *B. amphitrite** (including two subspecies; *: species examined in this paper), *B. subalbidus* Henry, 1973, *B. eburneus* Gould, 1814*, *B. improvisus* *, *B. variegatus*, *B. reticulatus**, *B. pallidus* Darwin, 1854, *B. albicostatus**, *B. kondakovi**, *B. citerosum* Henry, 1973, *B. suturaltus* Henry, 1973, *B. dentivarians* Henry, 1973, *B. patelliformis* Bruguière, 1789, *B. abeli* Lamy and André, 1932, *B. concavus* (including 4 subspecies), *B. venustus*, *B. poecilotheca*, *B. inexpectatus* Pilsbry, 1916, and *B. peruvianus* Pilsbry, 1909. Interspecific relationships were evaluated statistically using a generalized distance function and discrimination function analysis (Henry and McLaughlin, 1975).

Although considerable similarity in morphology exists among the taxa of the *B. amphitrite* complex, two natural groups can be recognized in the 19 species analyzed by Henry and McLaughlin (1975). The first group (*amphitrite* group of Henry and McLaughlin, 1975) is characterized by a multidenticulate labrum and includes *B. amphitrite*, *B. subalbidus*, *B. eburneus*, and *B. improvisus*. The second group (*pallidus* group of Henry and McLaughlin, 1975) is characterized by having subsidiary tubes in the parietes, a vesicular structure of the sheath, and complex setae on the inner face of cirrus III; it includes *B. pallidus*, *B. albicostatus*, *B. kondakovi*, *B. citerosum*, *B. suturaltus*, *B. dentivarians*, and, provisionally, *B. abeli* and *B. patelliformis*. The parietal tubes, the sheath, and the complex setae had been not described for these last two species and no material was available to Henry and McLaughlin (1975); however, these authors considered the ribbed shell and opercular valves to indicate close relationships with *B. albicostatus* and *B. kondakovi*, respectively. The remaining species among the 19 are distinguished by the absence of the diagnostic characters seen in the first two groups (except *B. inexpectatus*, which has complex setae on cirrus III); they can be divided into three subgroups based on similarities in general morphology: 1) the *concavus* group including *B. concavus* with its four subspecies; 2) the *variegatus* group including *B. variegatus* and *B. reticulatus*; and 3) the *venustus* group including *B. venustus*, *B. poecilotheca*, *B. inexpectatus*, and *B. peruvianus*.

To test the phylogenetic relationships among those species of the *B. amphitrite* complex of Henry and McLaughlin (1975) that inhabit the islands of Japan, we performed separate cladistic analyses of their morphology and the sequences of their mitochondrial cytochrome oxidase subunit I (COI) gene.

Materials and methods

1. Sampling

Four species of the *B. amphitrite* complex, *B. amphitrite* (8 specimens), *B. kondakovi* (6 specimens), *B. albicostatus* (7 specimens), and *B. eburneus* (8 specimens), were collected from Oikebajomae in northern Tokyo Bay. One species, *B. improvisus* (5 specimens), was collected from the Kasai Rinkai

Park in northeastern Tokyo Bay, *B. reticulatus* (6 specimens) was collected from Gushikawa, Okinawa Island, and *Tetraclita formosana* (2 specimens) was collected from Miyako Island, Okinawa. All specimens collected were immediately preserved in 95% ethanol.

2. Morphological characters and analysis

To analyze the phylogenic relationships of the six studied species of the *B. amphitrite* complex based on adult morphology, 11 morphological characters were selected for analysis: 1) those showing diverse and frequent occurrence among the species of the *B. amphitrite* complex; and 2) those shared by serially homologous structures (Table 1). The various states exhibited by these 11 morphological character were then polarized by using *Tetraclita formosana* Hiro, 1939 as an outgroup. A data matrix of phenotypic characters (Table 2) was set up and a Macintosh system was used to run the phylogenetic software program PAUP version 4.0b4a (Swofford, 2000). The branch-and-bound algorithm was used in this analysis, which guarantees the finding of the most parsimonious tree.

3. DNA extraction and PCR amplification

Mitochondrial DNA sequences were obtained from two specimens of each species of the *B. amphitrite* complex occurring in Japan. Tissue for total DNA extraction was isolated from the muscles of the trophi and cirri of each individual and digested overnight at room temperature in 500 µl TNES buffer. Following homogenization, 5 µl of proteinase K (100 µg/ml)

Table 1. Morphological characters and character states used in the cladistic analysis of six Japanese species of the *Balanus amphitrite* complex. *Tetraclita formosana* is an outgroup.

1. Parietes not smooth (0); smooth (1)
2. Basis of wall with numerous pores (0); pores not numerous (1)
3. Basis of longitudinal tube without subsidiary tube (0); with subsidiary tubes (1)
4. Labrum simple (0); multidenticulate (1)
5. Number of teeth on occludent margin of scutum < 5 (0); ≧5 (1)
6. Adductor ridge of scutum long (0); short to moderately long (1)
7. Crest of depressor muscle of tergum prominent (0); moderately prominent (1)
8. Articular furrow of tergum wide (0); narrow (1)
9. Spur furrow open (0); closed (1)
10. First maxilla with notch (0); without notch (1)
11. Mandible with 5th tooth confluent with inferior angle (0); not confluent (1)

Table 2. Morphological character matrix used in the cladistic analysis of six Japanese species of the *Balanus amphitrite* complex and the outgroup *Tetraclita formosana*.

Taxa	Characters										
	1	2	3	4	5	6	7	8	9	10	11
T. formosana (outgroup)	0	0	0	0	0	0	0	0	0	0	0
B. improvisus	1	1	0	1	1	1	0	0	1	1	0
B. reticulatus	0	1	0	0	1	0	1	1	1	0	1
B. amphitrite	0	1	0	1	1	1	0	0	1	1	0
B. eburneus	1	1	0	1	1	1	0	0	1	1	0
B. albicostatus	0	1	1	0	1	0	1	1	1	0	1
B. kondakovi	0	1	1	0	1	0	1	1	1	0	0

was added and digestion proceeded overnight at 55°C. The total genomic DNA was precipitated by adding 1 ml of cold 99% ethanol. Following washes in cold 70% ethanol, the DNA pellets were dried before being resuspended in TE buffer, pH 8.

DNA amplification was performed via the polymerase chain reaction (PCR). The primers used for amplification of one segment of approximately 600 base units of the COI mtDNA gene were: COI-B 5'-GGATGAACNGTNTAYCCNCC-3' (sense), COI-5R 5'-AAYACNTCNTTYTTYGAYCCNACNGGNGGN-3' (sense), COI-5 5'-NCCNCCNGTNGGRTCRAARAAN GANGTRTT-3' (antisense), COI-M 5'-GCRATRAT NGCRTARATYATNCC-3' (antisense), and COI-A 5'-AGTCARCTRAANACTTTAAT-3' (antisense). The terminal nucleotides at the 3' end of each primer are comparable to the mtDNA sequence of *Drosophila yakuba* (Clary and Wolstenholme, 1985). The mixtures for amplification (50 μl) contained 5 μl of the "Gene Release" products [1 μl of extracted DNA + 20 μl "Gene Releaser" (BioVentures, Inc.)], 20.5 μl of sterile distilled H_2O, 3 μl of 25mM $MgCl_2$, 5 μl of 2mM dNTPs, 5 μl of each primer, 5μl buffer, and 0.5 μl Taq DNA Polymerase (TOYOBO Co. LTD.). The PCR treatment was carried out under the following conditions: denaturation for 40 sec at 92°C, annealing for 1 min at 50°C, and extension for 1 min at 72°C; the entire sequence was repeated 30 times.

4. DNA sequencing

The double-stranded DNA fragments produced by PCR were purified and concentrated by ultrafree-MC Millipore filtration, and the pellets obtained were dissolved in 40 μl of sterile distilled water. A portion (4.5 μl) of each sample was treated with dye-labeled terminators and sequenced.

5. Sequence alignment and phylogenetic analysis

The barnacle DNA sequences were aligned with the mitochondrial sequence of *Artemia franciscana* (Valverde *et al.*, 1994). They were aligned manually, and gaps caused by inferred insertion and/or deletion events, and regions with ambiguity in alignment, were excluded from analysis. Amino acid translations of the nucleotides were also carried out by using the mtDNA genetic code of *A. franciscana* (Valverde *et al.*, 1994). Genetic distance estimations and reconstructions of phylogenetic trees were made by application of the maximum parsimony (MP) method using the computer package PAUP version 4.0b4a. The branch-and-bound search algorithm and equal weighting for all substitutions were employed. All phyloge netically uninformative sites were neglected. To evaluate the robustness of the internal branches, 500 bootstrap replications were executed. The Kimura 2-parameter distance method (Kimura, 1980) was used to generate phylogenetic trees by the neighbor-joining (NJ) method (Saitou and Nei, 1987). Estimates of nucleotide sequence divergence and the number of transition and transversion substitutions were determined by the method of Jukes and Cantor (1969). The mtDNA sequence used for *Tetraclita formosana* was taken from the work of Hasegawa *et al.* (1996).

Results

1. Cladistic analysis of the morphological characters

The most parsimonious cladogram (tree) found had 12 steps, a Consistency Index (CI) of 0.917, and a Retention Index (RI) of 0.923 (Fig. 2). This fully resolved tree split into two main clades (at node 12), one including *B. amphitrite*, *B. eburneus*, and *B. improvisus*, the other comprising *B. reticulatus*, *B. kondakovi*, and *B. albicostatus*. Furthermore, two pairs of species with close phylogenetic relationships (sister taxa) appear in this tree, *B. eburneus* and *B. improvisus* at node 10, and *B. kondakovi* and *B. albicostatus* at node 8.

2. Sequence variation

In the present study sufficient sequencing data for analysis were obtained from reference positions 1872-2424 of the complete mitochondrial DNA of *A. franciscana* (Valverde *et al.*, 1994) and all taxa examined (Appendix). The sequences of all taxa examined will be deposited in the DDBJ (DNA Data Bank of Japan). The 552 base pairs of the COI gene contained 184 informative sites distributed evenly over the length of the sequence. One amino acid deletion was observed at position 152 in *B. amphitrite*, and another at position 83 in *B. kondakovi*. Two three-amino-acid deletions were observed at positions 78, 82, and 170 in *B. reticulatus* and at positions 11, 42, and 64 in *B. eburneus*.

All base pair changes occurred in the first or third positions of codons, and three of them caused an amino acid replacement at positions 73, 133, and 177. The average nucleotide composition was A = 25.5%, T = 38.6%, C = 17.3%, and G = 18.5%. The most frequently used nucleotide was thymine (range 37.4-42.4%), and cytosine was the least frequently used, this being comparable to the composition of the mitochondrial protein genes of other invertebrate phyla (Wolstenholme, 1992).

The numbers of transition and transversion substitutions are shown in Table 3; the ratio between them ranges from 0.56 to1.49 for each species pair, values considerably less than the value for mammals, 2.0 (Nei, 1987).

Distance values and uncorrected pair-wise percentage differences among the six species and the outgroup taxon are given in Table 4. The pair-wise estimates of sequence divergence between species pairs range from

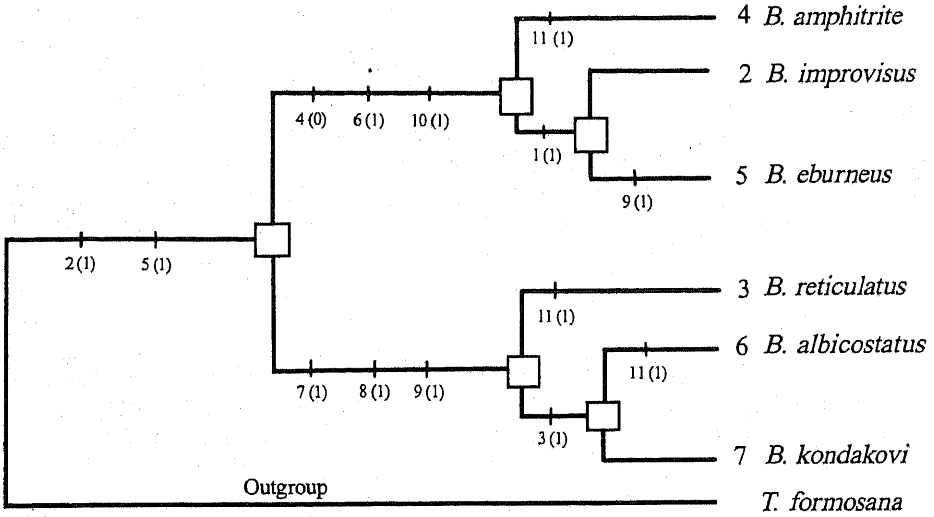

Fig.2. Cladogram based on morphological characters illustrating a hypothesis of relationships among six Japanese species of the *Balanus amphitrite* complex; CI= 0.917 and RI= 0.923. For character codes see Table 1.

2.58% (*B. eburneus* and *B. improvisus*) to 21.42% (*B. albicostatus* and outgroup). The ingroup uncorrected differences range from 0.62 to 2.28%, while those between the ingroup and outgroup range from 2.18 to 2.45%.

3. Cladistic analysis of the mtDNA sequences

The NJ analyses based on Kimura 2-parameter distances produced a single most parsimonious and fully bifurcating tree (Fig. 3). All of the internal branches were supported by remarkably high bootstrap proportions (89-96%) for all transition/transversion weighting schemes. The MP method, using the Kimura-2 parameter distance model of sequence evolution, produced the same tree (Fig. 4) as the NJ method, with all internal branches supported by high (> 88%) bootstrap probabilities. When conditions are favorable for phylogenetic analysis (*i.e.*, equal and appropriate rates of change, and symmetrical phylogenies), bootstrap probabilities (sometimes misleadingly called "bootstrap P values") are highly conservative measures of the probability that the corresponding clade is true (Hillis and Bull, 1993). All of the constructed phylogentic trees had two major clusters: one composed of *B. amphitrite*, *B. improvisus*, and *B. eburneus*, and the other of *B. reticulatus*, *B. kondakovi*, and *B. albicostatus*.

Table 3. Transition/transversion ratios for COI sequence data Pair-wise comparisons among six species of the *Balanus amphitrite* complex and the outgroup *Tetraclita formosana.*

OTUs	*B. improvisus*	*B. reticulatus*	*B. amphitrite*	*B. eburneus*	*B. albicostatus*	*B. kondakovi*	*T. formosana*
B. improvisus		1.37	0.7	0.56	1.38	1.28	1.4
B. reticulatus			1.21	1.34	0.79	1.06	1.17
B. amphitrite				0.67	1.26	1.36	1.24
B. eburneus					1.49	1.33	1.31
B. albicostatus						1.08	1.13
B. kondakovi							1.09
T. formosana							

Table 4. Genetic distances and uncorrected differences from COI sequence data calculated by the Jukes-Cantor method (Jukes and Cantor, 1969) between all pairs of analyzed species of the *Balanus amphitrite* complex and the outgroup *Tetraclita formosana*. Upper-right matrix: genetic distance, lower-left matrix: uncorrected difference, both expressed as percentages.

OTUs	*B. improvisus*	*B. reticulatus*	*B. amphitrite*	*B. eburneus*	*B. albicostatus*	*B. kondakovi*	*T. formosana*
B. improvisus		16.57	6.2	2.58	16.97	19.16	18.37
B. reticulatus	2.19		15.88	16.55	12.53	12.54	18.8
B. amphitrite	1.14	1.82		5.53	19.05	18.13	18.79
B. eburneus	0.62	2.07	1.07		16.96	18.43	19.07
B. albicostatus	2.02	1.61	2.18	2.07		9.52	21.42
B. kondakovi	2.28	1.69	2.09	2.21	1.27		20.29
T. formosana	2.18	2.25	2.26	2.25	2.45	2.4	

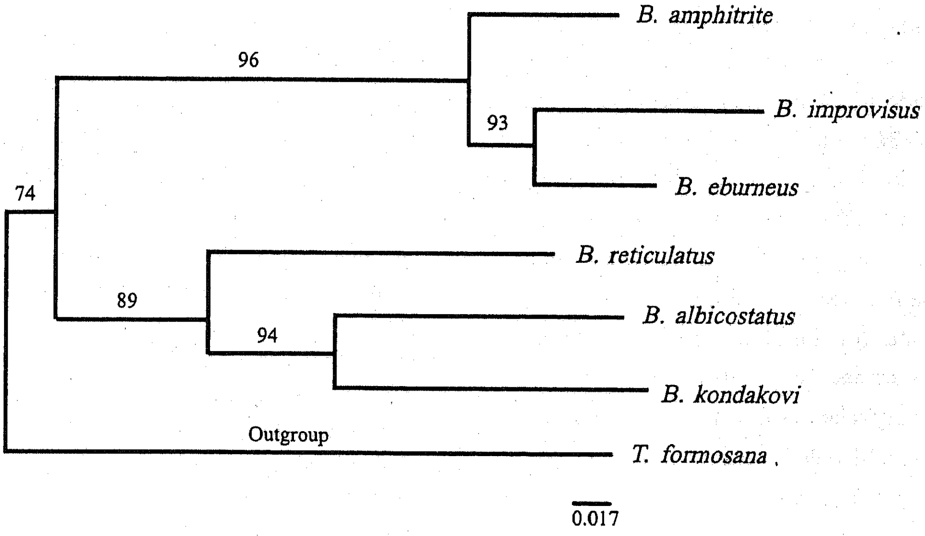

Fig. 3. Branch-and-bound bootstrap tree for COI sequence data from six Japanese species of the *Balanus amphitrite* complex. The tree is based on genetic distances calculated by the Kimura 2-parameter method (Kimura, 1980) using the NJ method (Saitou and Nei, 1987), based on 552 nucleotide positions with 500 bootstrap replicates. Branch length reflects relative genetic distance.

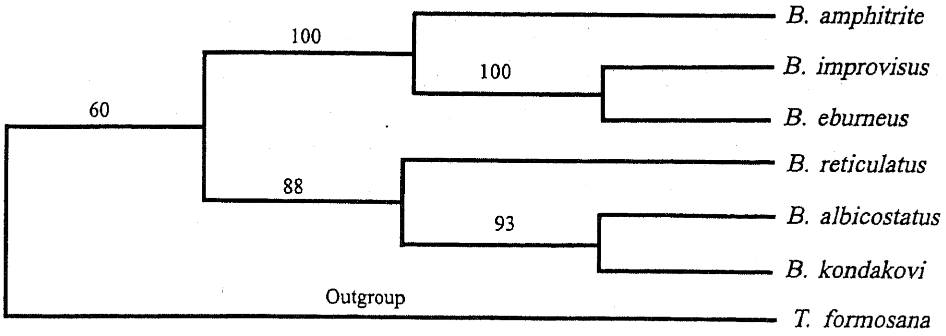

Fig. 4. Branch-and-bound bootstrap tree for COI sequence data from six Japanese species of the *Balanus amphitrite* complex using the MP method. The tree was constructed based on 552 nucleotide positions with 500 bootstrap replicates.

Discussion

In grouping 16 species of the *B. amphitrite* complex based on morphological characters, Henry and McLaughlin (1975) found that *B. amphitrite*, *B. eburneus*, and *B. improvisus* were readily separable from *B. reticulatus*, *B. kondakovi*, and *B. albicostatus*, and this is in agreement with the present findings (Figs 2-4).

The maximum uncorrected percentage difference was less than 2.28% among the ingroup species. The present mitochondrial DNA data demonstrated that sufficient sequence divergence exists (Table 4; 0.62%-2.28%) to resolve the species-level phylogeny in the *B. amphitrite* complex. The present phylogenetic analysis leads us to the following conclusions.

Two different groups can be distinguished within the *B. amphitrite* complex. The early evolutionary history of this group is characterized by divergence into two major basal lineages: the first clade, comprising three species (*B. amphitrite*, *B. eburneus*, and *B. improvisus*), and the second clade, also comprising three species (*B. reticulatus*, *B. kondakovi*, and *B. albicostatus*). Moreover, a consideration of morphological characters, specifically the labrum, shell structure, and characteristics of cirrus III, favors the grouping of these two groups together within the *B. amphitrite* complex.

Sequencing data for the other species of the *B. amphitrite* complex are necessary to determine more precisely the evolutionary relationships within the complex in order to make more detailed comparison with Henry and McLaughlin's (1975) findings.

Darwin (1854) noted that the barnacles later called *Balanus concavus mexicanus* Henry, 1941 had a closer affinity with *Balanus amphitrite* than with what he thought was living *B. concavus* from Panama. Perhaps for this reason, Henry and McLaughlin (1975) included *B. concavus sinensis* Broch, 1931, *B. c. indicus* Nilsson-Cantell, 1932, and *B. c. pacificus* Pilsbry, 1916, as well as *B. c. mexicanus*, in the *B. amphitrite* complex. Newman and Ross (1976) placed *B. c. mexicanus* and a few other living forms in the largely extinct Group of *B. concavus*, but Newman (1982), in redefining this Group noted a closer affinity of *B. pacificus* and *B. mexicanus* to the Group of *B. amphitrite*. However, when Zullo (1992) revised the fossil and living species attributed to *Concavus* Newman, 1982 and its subgenera, he not only elevated the subgenera to full generic status, but he also proposed a new genus, *Paraconcavus*, for *B. pacificus* and *B. mexicanus*, and assigned it to his new subfamily, the Concavinae. It may be hoped that future molecular as well as morphological phylogenetic work will shed light on these relationships.

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Appendix

Nucleotide and deduced amino acid sequences of partial COI mtDNA. Identical nucleotides with those of first sequence denoted by dots, identical amino acids with those of first sequence denoted by asterisks. Questions marks represent missing data.Four-digit numbers above sequence correspond to the positions of the homologous nucleotides in *Artemia franciscana* (Valverde *et al.*, 1994); amino acid sequence of *Tetraclita formosana* from Hasegawa *et al.* (1996).

```
                                                     1900
                  I   A   H   S   G   A   S   ?   E   L   S   I   F   S   L   H   L   A   G   A   S   S   I   L   G   A   I   N   F   M
B. amphitrite    ATT GCT CAC TCG GGT GCT TCA GT? GAA CTG TCC ATC TTC TCT CTG CAC TTA GCT GGT GCA TCT TCC ATT CTA GGC GCA ATC AAT TTT ATG
                  *   *   *   *   *   *   *   V   D   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. improvisus    ... ..A ..T ..A ..A ... ... ..T ..T T.. ..T ..T ... ... T.. ..T ... ..G ..A ..T ... ..T ..C ..G ..G ..T ..T ... ... ..A
                  *   *   *   *   *   *   *   V   D   *   ?   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. eburneus      ... ..A ..T ..A ..A ... ... ..T ..T T.. ?.T ..T ... ... T.. ..T ..G ..G ..A ..T ... ..T ..C ..G ..A ..T ..T ... ... ..A
                  *   *   *   *   *   *   V   D   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. reticulatus   ... ..A ..T ... ... ... ... ..T ..C T.A ..T ..T ..T ... T.. ..T ..G ... ... ..T ... ..T ... ... ..T ..T ..T ..C ... ..A
                  *   *   *   *   *   *   *   V   D   *   *   *   *   *   *   ?   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. albicostatus  ... ... ..T ... ... ... ..T ..G ..C T.A ..A ..T ..T ..A T.A ??? ... ..A ..A ..T ... ..T ..C T.. ..A ..T ..T ... ... ..A
                  *   *   *   *   *   *   *   V   D   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. kondakovi     ... ... ..T ..A ... ... ..T ..T ..C T.A ..T ..T ..T ... T.A ..T ..G ..A ..G ..T ... ... ..C T.. ... ..T ..T ..C ... ..A
                  *   *   *   *   *   *   *   V   D   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
T. formosana     ... ..C ... ..A ..A ... ... ..A ..T T.A ..T ... ... ... ..C ... C.. ... ..G ..T ... ... ... T.. ..G ... ... ... ... ..A
                  *   *   *   A   *   P   *   V   D   *   A   *   *   *   *   *   *   *   *   V   *   *   *   *   *   *   V   *   *   I
A. franciscana   ... ..C ..T G.C ..A C.. ..T ..A ..T T.A G.T ..T ... ..G ..T ..T ... ... ..A .TT ..C ..T ..C T.. ..G ..T G.A ... ... ..T

                                                                 2000
                  S   T   V   I   N   M   R   A   E   T   L   T   F   D   R   L   P   L   F   V   W   S   V   L   M   T   V   I   L   L
B. amphitrite    TCC ACA GTT ATC AAC ATA CGA GCA GAG ACC TTA ACA TTT GAC CGT TTA CCA TTA TTT GTC TGA AGA GTC TTA ATG ACT GTA ATT CTT CTG
                  *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *
B. improvisus    ..T ... ..A ..T ..T ... ..G ..T ... ..A ..G ..T ..C ... ... C.C ..T ... ... ..T ... ..T ..G ..C ..A ..C ..T ..C ..A ..A
                  *   *   *   *   *   *   *   *   *   *   *   ?   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *
B. eburneus      ..T ..C ... ..T ..T ... ..G ... ... ..T ..G ..? ..C ... ..A C.C ..T ... ... ..T ... ..T ..A ..T ..A ... ..T ..C ... ..A
                  *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *
B. reticulatus   ..A ..T ..A ..T ..T ... ..G ... ..A ..A ... ... ... ..T ..A C.C ..T ... ... ..T ... ... ... ..T ... ... ..T ... T.A T..
                  *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *
B. albicostatus  ..T ..T ... ... ..T ... ..G ... ..A ..A ... ... ... ... ..A C.T ..T ... ..C ..A ... ..T ..A ..T ... ..A ... ... ... T..
                  *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *
B. kondakovi     ..T ..T ..C ..T ..T ... ... ... ... ..A ... ... ... ... ... C.. ..T ... ... ..T ... ..T ..A ..T ... ..A ... ... T.G T..
                  *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   F   L   *   *   *   *   *
T. formosana     ..A ... ... ..T ... ... ... ..C ..A ..T C.. ..T ... ..T ... C.T ..C ... ... ..T ... ... ..T ..C ..T ... ..T ... ... ..T
                  T   *   I   *   *   *   *   P   Q   S   M   S   I   *   *   M   *   *   *   *   *   A   *   G   I   *   A   V   *   *
A. franciscana   A.T ..T A.C ..T ..T ... ... C.C C.. T.A A.. T.T A.. ... ... A.. ..T C.C ..C ... ... GC. ..A GG. ..C ..C .CC G.. ... ..C

                                                                             2100
                  L   L   S   L   P   V   L   A   G   A   L   T   M   L   L   T   D   R   N   L   N   T   S   F   F   D   P   T   G   G
B. amphitrite    TTA CTA TCA TTA CCA GTA TTA GCA GGA GCT CTT ACT ATG CTT TTA ACA GAC CGG AAT TTA AAT ACT TCC TTC TTT GAT CCA ACA GGA GGT
                  *   *   *   *   *   *   *   *   *   *   I   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. improvisus    C.T T.. ..T C.. ..T ..T C.T ..T ..G ..A A.. ... ..A ... ..G ..G ..T ..A ... ..G ... ... ..T ... ... ... ... ..T ... ..G
                  *   *   *   ?   *   *   *   *   *   *   I   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. eburneus      C.T T.. ..T ??? ... ..T C.T ... ..G ..A A.. ... ..A ..A ... ..G ..T ..T ... ..G ... ... ..T ... ... ... ... ..T ... ..G
                  *   *   *   *   *   *   *   *   *   *   I   *   *   *   *   *   *   ?   *   *   *   ?   *   *   *   *   *   *   *   *
B. reticulatus   ... ... ..T ... ... ... ... ... ... ... A.. ... ..A ... ..G ..G ..T ??? ... ..G ... ??? ..G ..T ... ... ..T ..C ... ..A
                  *   *   *   *   *   *   *   *   *   *   I   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. albicostatus  C.G ... ... ... ... ... ... ... ... ... A.. ... ..A ..A ... ..T ..T ... ... ..G ... ... ..A ..T ... ... ..T ... ... ..A
                  *   *   *   *   *   *   *   *   *   *   I   *   *   *   *   *   *   *   *   *   *   *   ?   *   *   *   *   *   *   *
B. kondakovi     C.G ... ..T ... ... ... ... ..T ... ... A.. ... ... ... ... ..T ..T ... ... ..G ... ... ??? ..T ... ... ..T ..G ..G ..A
                  *   *   *   *   *   *   *   *   *   *   I   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
T. formosana     C.C T.G ..T C.. ... ..T C.. ... ... ... A.C ..A ..A ..C ..G ... ... ..A ..C C.T ... ..A ... ... ..C ..C ..G ... ..C ..A
                  *   *   *   *   *   *   *   *   *   *   I   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   A   *   *
A. franciscana   C.T T.. ... C.T ... ..C C.. ..G ..G ... A.. ... ..A ..G ... ..T ..T ..T ..C ... ... ... .TT ..T ..C ..C ..C G.. ..T ...
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Appendix. (continued)

```
                                                                          2200
                   G   D   P   I   L   Y   Q   H   L   F   C   F   F   G   H   P   E   V   Y   I   L   I   L   P   A   F   G   M   I   S
B. amphitrite     GGT GAC CCT ATT TTA TAC CAG CAC TTA TTT TGT TTT TTT GGA CAT CCT GAA GTC TAT ATT TTA ATC TTG CCT GCT TTT GGT ATA ATC TCT
                   *   *   *   *   *   *   *   *   *   *   W   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. improvisus     ... ... ... ... ... ... ..A ..T ... ... ..G ... ... ..G ... ..G ... ..T ..C ... ..G ..T ..A ..G ... ... ..A ... ... ..C
                   *   *   *   *   *   *   *   *   *   *   W   *   *   *   *   *   *   *   *   *   *   ?   *   *   *   *   *   *   *   *
B. eburneus       ... ... ... ... ... ... ..A ... ... ... ..G ... ... ... ... ..G ... ..T ..C ... ..G ..? ..A ..G ... ... ..A ... ... ..A
                   *   *   *   *   *   *   *   *   *   *   W   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. reticulatus    ... ..T ... ... C.. ..T ..A ..T ... ... ..A ... ... ..T ... ... ..G ..T ... ... ... ..T ..A ... ... ... ..A ... ... ..A
                   *   *   *   *   *   *   *   *   *   *   W   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. albicostatus   ... ..T ..A ... ... ..T ..A ..T ... ... ..A ... ... ... ... ... ..G ..T ... ... ... ... ..A ... ... ... ... ..G ..T ...
                   *   *   *   *   *   *   *   *   *   *   W   L   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. kondakovi      ... ... ..A ... ... ..T ..A ..T C.. ... ..A ..A ... ..T ... ... ... ... ... ... ... ... ... ..G ..A ... ... ... ..T ...
                   *   *   *   *   *   *   *   *   *   *   W   *   *   *   *   *   *   *   S   *   *   *   *   *   *   *   *   *   *   *
T. formosana      ..A ... ... ... C.T ... ..A ..T ... ... ..A ..C ... ..T ..C ..G ... ..T .CA ... ... ..T C.T ..A ..C ... ... ... ... ...
                   *   *   *   *   *   *   *   *   *   *   W   *   *   *   *   *   *   *   *   *   *   *   *   *   G   *   *   *   V   *
A. franciscana    ..G ..T ..C ..C C.T ..T ..A ..T ... ... ..A ... ... ..C ... ... ... ..G ... ... ... ..T ..A ... .GA ..C ..G ... G.G ..C

                                                                                              2300
                   H   I   V   A   S   E   S   G   K   K   E   S   L   G   T   L   G   M   I   Y   A   I   I   A   I   G   I   L   G   F
B. amphitrite     CAT ATT GTG GCA AGT GAA AGT GGA AAG AAG GAA TCT TTG GGA ACC TTA GGT ATG ATT TAC GCA ATC ATT GCT ATT GGT ATT TTA GGA TTT
                   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. improvisus     ... ... ... ..T ... ... ... ..T ... ... ... ... ... ... ..T ... ... ... ... ... ..T ..T ... ... ... ... ... ... ... ...
                   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. eburneus       ... ... ... ..T ..C ... ... ... ... ... ... ... ... ... ..T ... ... ... ... ... ... ..T ... ... ... ... ... ... ..T ...
                   *   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *   *   H   *   V   *   S   E   S   G   K   K
B. reticulatus    ... ... ..A ..T ..A ... ..A ..G ..A ..A ..G ... ..T ... ... C.. ..G ... ... ..T CAT ..T G.A ... .GA .AA .GA GGG AA. AAA
                   *   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. albicostatus   ... ... ..A ..T ... ..G ... ... ..A ..A ... ... ..T ... ..T C.G ..A ..A ... ..T ... ..T ... ... ... ..A ... ... ... ...
                   *   *   *   *   *   *   *   *   *   *   *   *   F   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. kondakovi      ... ..C ..A ..T ... ..G ..A ..G ..A ..A ... ... ..T ... ..T C.. ..A ... ... ..T ..T ..T ... ..A ... ..A ... ..G ... ...
                   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   M   *   *   *   *   *   *   *   *   *
T. formosana      ... ... ... ... ..A ... ..A ... ..A ..A ... ..C ... ... ... ... ..C ... ... ... ... ..A ..C ... ... ..A ... ..G ... ...
                   *   *   I   S   Q   *   *   *   *   *   *   A   F   *   *   *   *   *   *   *   M   L   *   *   *   *   *   *   *   *
A. franciscana    ..C ... A.T AGC CAA ... ..A ..T ... ... ... G.A ..T ..T ..A ... ... ... ... ..T ..T ..A C.. ..A ... ... ... C.T ..T ...

                                                                                                                      2400
                   V   V   W   A   H   H   M   F   T   V   G   M   D   V   D   T   R   A   Y   F   T   S   A   T   M   I   I   A   V   P   T   G   I   N
B. amphitrite     GTG GTA TGA GCA CAT CAC ATG TTC ACC GTA GGA ATG GAC GTT GAT ACG CGA GCA TAC TTT ACG TCC GCT ACT ATA ATT ATC GCA GTC CCA ACA GGG ATT AAT
                   *   ?   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   D   *   *   *   M   *   *   *   *   *   *   *
B. improvisus     ... ??? ... ... ..C ..T ... ..T ..T ... ... ..A ... ... ... ..T ... ..T ... ... ..A ... .A. ... ... ... ..A ..G ... ... ..C ... ... ...
                   *   *   *   *   *   *   *   L   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. eburneus       ... ... ..G ... ..C ..T ... ..A ... ... ... ..A ... ... ... ..T ... ... ... ... ... ... ... ... ... ... ... ... ... ... ..C ... ... ...
                   E   S   F   G   T   L   G   M   I   Y   *   *   *   *   *   *   *   *   *   ?   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. reticulatus    .A. TCT .TT .G. ACC .TA GG. A.G .TT TAT ..T ..A ..T ... ... ..A ... ..T ..T ?.. ..A ..T ... ... ... ... ..T ..T ..T ..T ... ... ... ...
                   *   *   *   *   E   D   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   T   *   *   *   *   *   *   *   *   *   *   *
B. albicostatus   ..A ... ... ..T G.G G.T ..A ..T ..A ... ... ..A ... ... ... ..T ... ... ..T ..C ..A ..T A.. ... ... ... ..T ..T ..T ..T ..T ... ... ...
                   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *
B. kondakovi      ..A ... ... ..T ..C ..T ... ..T ..A ... ..T ..A ... ... ... ..T ..T ... ..T ..C ..A ..T ..A ... ... ... ..T ..T ..A ..T ..T ... ... ...
                   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   ?   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   K
T. formosana      ..A ... ... ..T ..C ..T ... ..T ..A ... ... ... ... ... ... ... ... ..? ... ... ..T ..T ..A ... ... ... ..T ..T ..T ... ... ... ... ..A
                   *   ?   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   *   A   *   *   *   *   *   *   I   *   *   *   *   K
A. franciscana    ..T ..C ..G ..T ... ..T ..A ..T ..T ..G ... ... ... ..G ..C ..T ... ..T ..T ... ..T G.T ..A ... ..G ... ..T ... A.T ..T ..G ... ... ..G
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Balanus thailandicus sp. nov., a new mangrove barnacle of the *Balanus amphitrite* complex (Cirripedia, Balanomorpha) from Satun, Southwest Thailand

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Abstract

A new mangrove barnacle, *Balanus thailandicus* sp. nov., is described from the Puyu Canal, Tamalung Bay, Satun, southwest Thailand. The new species has the common characteristics of the *Balanus amphitrite* complex and is more or less sympatric with *B. reticulatus, B. amphitrite, B. patelliformis*, and *B. variegatus*. *Balanus thailandicus* is most similar to *B. reticulatus*, but it is clearly distinguishable from the last three mentioned species of the complex in having the parietes folded or ribbed in adults but smooth in juveniles, parietal tubes solid in the upper half and interrupted by transverse septa in the lower part, the large number of articles in the anterior ramus of cirrus I, and erect hooks below the posterodistal angles of the articles of cirri III and IV.

Key words: *Balanus thailandicus*, new species, morphology, phylogeny, Thailand

Introduction

During systematic studies on the living barnacles of Satun, southwestern Thailand, a new form was found attached to prop roots of mangrove trees in estuarine or brackish water conditions. This barnacle is interpreted as being closely related to some species of the *B. amphitrite* complex. In this paper, the morphological characteristics of the new species are described and compared with those of other members of this complex.

Systematic Description

Subclass Cirripedia Burmeister, 1834
Order Thoracica Darwin, 1854
Suborder Balanomorpha Pilsbry, 1916
Superfamily Balanoidea Leach, 1817 (*sensu* Newman & Ross, 1976)
Family Balanidae Leach, 1817
Genus *Balanus* Da Costa, 1778
Balanus amphitrite complex Henry & McLaughlin, 1975

Balanus thailandicus sp. nov. (Figs. 1-3)

Diagnosis

Shell conical to subcylindrical; parietes with ribbed, folded, or smooth surface, cross-hatched by longitudinal and transverse purplish bands; radii narrow to moderately wide; summits oblique. Cavity beneath sheath filled in with calcareous matter. Parietal tubes in single row, without subsidiary tubes, solid in upper half and with transverse septa in lower part. Scutum with long adductor ridge separated from articular ridge. Tergum with convex carinal margin; spur furrow open, and spur rounded at its end; basal margin usually straight on either side of spur. Labrum simple with 3-4 teeth on either side of notch. Cirrus I with more articles on anterior ramus than in some other members of the *Balanus amphitrite* complex. Articles of cirrus III without complex setae. Cirri III and IV with a hook below posterodistal angle of each article.

Table 1. List of specimens examined. Length: rostro-carinal diameter, Width: carino-lateral diameter (in mm).

Type	Depository	Cat. Or Reg. No.	Length (L)	Width (W)	Height (H)
second paratype	SIO	BIC10241	12.1	11.4	6.8
third paratype	BMNH	2000.1777	17.4	16.8	14.6
fourth paratype	NSMT	Cr13223	14.5	13.4	8.3
fifth paratype	NSMT	Cr13224	14.7	11.2	12.1
sixth paratype	USNM	306584	11.8	16.3	7.5
seventh paratype	NSMT	Cr13225	14.7	12.4	5.7
eighth paratype	RUI	B2000.503	23.9	20.7	14.1
ninth paratype	USNM	306585	17.1	16.4	14.1
Holotype	NSMT	Cr13221	19.1	21.2	11.6
tenth paratype	BMNH	2000.1778	15.8	19.1	11.1
first paratype	NSMT	Cr13222	14.8	17.3	13.1
eleventh paratype	RUI	B2000.501	18.9	13.2	12.8
twelfth paratype	RUI	B2000.502	20.1	17.2	11.2

Materials

Thirteen specimens collected from the Puyu Canal (type locality; 6°59'N, 100°13'E), Tamalung Bay, Satun, southwestern Thailand, by one of us (TY) on May 11, 1999. The holotype and 12 paratypes have been deposited in the National Science Museum, Tokyo (NSMT), Scripps Institution of Oceanography, La Jolla (SIO, Benthic Invertebrates), the National Museum of Natural History, Washington D.C. (USNM), The Natural History Museum, London (BMNH), and the Riau University, Indonesia (RUI, Benthic Invertebrates) (Table 1). Length is the rostro-carinal diameter, and width is the carino-lateral diameter, in mm. In this study, the morphological terms used by Henry & McLaughlin (1975) and Newman & Ross (1976) were adopted except for teeth on articles of cirri.

Habitat. The new species was found intertidal, predominantly on the stems and prop roots of mangrove *Rhizophora apiculata*, but also on *Rhizophora mucronata* and mangrove *Avicennia officinalis*, in the Puyu Canal (type locality) and Tachin Canal (near type locality), Tamalung Bay, Satun, SW Thailand. The salinity during high tide in the Puyu and Tachin Canals is shown in Table 2. This new species was associated with *Chthamalus* sp., *Balanus amphitrite*, *B. variegatus*, and *B. rhizophorae*.

Description

Shell (Fig. 1A-B) conical to subcylindrical, with smooth surface in juvenile and ribbed or folded surface in adult. Orifice toothed, width usually more than 1/2 rostro-carinal diameter. Color of parietes white or dull-purplish brown, with dark purple longitudinal stripes crossed by many horizontal reddish-brown and white lines. Apex of carina often turned outward. Radii narrow to moderately wide with horizontal striae; summits oblique, thick, moderately disparietal, rough, sutural edges denticulate; color of radii white or bluish. Alae with summits nearly parallel to the base, sutural edges denticulate, dirty brown near parietes, white near sutures. Cavity between sheath and inner lamina filled in with calcareous matter (Fig. 2A). Inner lamina ribbed near base; ribs often extending from denticulations near basis to sheath. Parietal tubes in single row, filled by calcareous matter in their upper half, with transverse septa in the lower parts (Fig. 2A). Inner surface of outer lamina with fine longitudinal ribs. Basis thin, with radial tubes extending nearly to periphery.

Opercular plates (Fig. 1C-F). Scutum usually flat except for being reflexed at apex, sometimes externally concave between apex and basal margin; tergal segment narrowly inflected; basitergal angle obliquely truncated; occludent margin moderately toothed; growth ridges low to moderate, finely crenulated; longitudinal striae fine, sometimes indistinct. Inner surface of scutum mostly smooth, occasionally roughened near apex; articular ridge high, reflexed at about 3/5 length of tergal margin and at about 1/3 length of occludent margin; articular furrow deep; adductor ridge moderate, usually with shallow pit below, clearly separated from articular ridge; adductor muscle pit distinct; lateral depressor muscle pit small, shallow, sometimes absent. Color of scutum externally usually brownish purple with narrow white band along tergal margin; inner surface usually grayish

Table 2. Salinity of Puyu and Tachin Canals at high tide (in ppt).

Location / Date	Nov., 1995	March, 1996	March, 1999
Puyu Canal			
upstream	22	30	25
middle	24	30	28
downstream	26	30	30
Tachin Canal			
upstream	13	26	20
middle	19	29	25
downstream	23	30	30

lavender with white tergal segment, occasionally purplish with white articular and adductor ridges.

Tergum with raised, moderately denticulate scutal margin; carinal margin slightly convex; growth ridges low to moderate, usually crenulated, with longitudinal striae occasionally present on carinal side; basal margin usually straight on both sides of spur; spur furrow open; spur broadly rounded at end; spur width about 1/5 length of basal margin; spur length about 5/4 spur width. Internally, scutal margin low; articular ridge moderately prominent, reflexed at apex; articular furrow deep; crests of depressor muscles long, prominent, numerous (5-8), projecting slightly beyond basal margin; surface sometimes roughened on upper part, smooth near base. Color of tergum externally mostly brownish purple with white spur furrow, usually purple internally except for white spur margins, articular ridge, and crests of depressor muscle.

Mouthparts. Labrum (Fig. 3A) with setulae and 3-4 teeth on either side of notch. Palps with short pinnate setae on upper margin and in narrow band near upper margin of outer face, and long setae on lower half of distal margin and in oblique row near distal angle. Mandible (Fig. 3B) with 5 teeth; inferior angle spinose; 4th tooth occasionally bifid or with extra denticle; 5th tooth usually confluent with inferior angle. First maxilla (Fig. 3C) with small notch, including 2 or 3 fine spines, below upper pair of spines; 6-7 spines between this notch and last pair of spines at maxilla's inferior angle. Second maxilla bilobed with setae on distal margin of distal lobe and pinnate setae near lower margins of both lobes.

Cirri. Protopods of anterior cirri with finely pinnate setae primarily on anterior margins and distal sutures; basipodite of cirrus I with narrow band of multifid spinules near posterior margin on outer face; protopods with simple spinules below posterodistal angle; basipods of cirri II and III with narrow band of simple spinules below distal articulations. Mean and range in number of articles of rami of right cirri shown in Fig. 4.

Cirrus I (Fig. 3D) with anterior ramus longer than posterior one and with larger number of articles than later (18-26). Posterior ramus with protuberant articles; proximal articles of anterior ramus also protuberant. Distal sutures of both rami with long setae and multifid spinules.

Cirrus II (Fig. 3E) with anterior ramus nearly equal to posterior ramus in length and number of articles; articles of both rami moderately protuberant; anterior and posterior margins of medial and proximal articles with multifid spinules, and distal articulations with simple spinules.

Cirrus III (Fig. 3F-G) with anterior ramus slightly shorter than posterior ramus in both length and number of articles; articles of both rami slightly protuberant; inner faces of distal sutures occasionally with numerous simple setae or spinules. Anterior and anterodistal margins of each article with conical denticles (denticles correspond to the "conical teeth" of Henry and McLaughlin (1975) that are not true teeth) and 4-6 pairs of setae of medium length. Posterior margin with 2 or 4 relatively long setae and an erect hook (hooks correspond to the "erect teeth" of Henry and McLaughlin (1975) that are not true teeth) below posterodistal angle of each article. Posterior margins of articles of anterior ramus with simple spinules. Rami without complex setae, usually with 1-2 pectinate setae and occasionally with 1 or 3 bifurcate setae on medial articles.

Cirrus IV (Fig. 3H) with simple spinules on anterior margin of each article, but no conical denticles; armed with poorly developed spines on posterodistal angle, multifid spinules below posterodistal spines and along distal sutures of articles, and an erect hook below

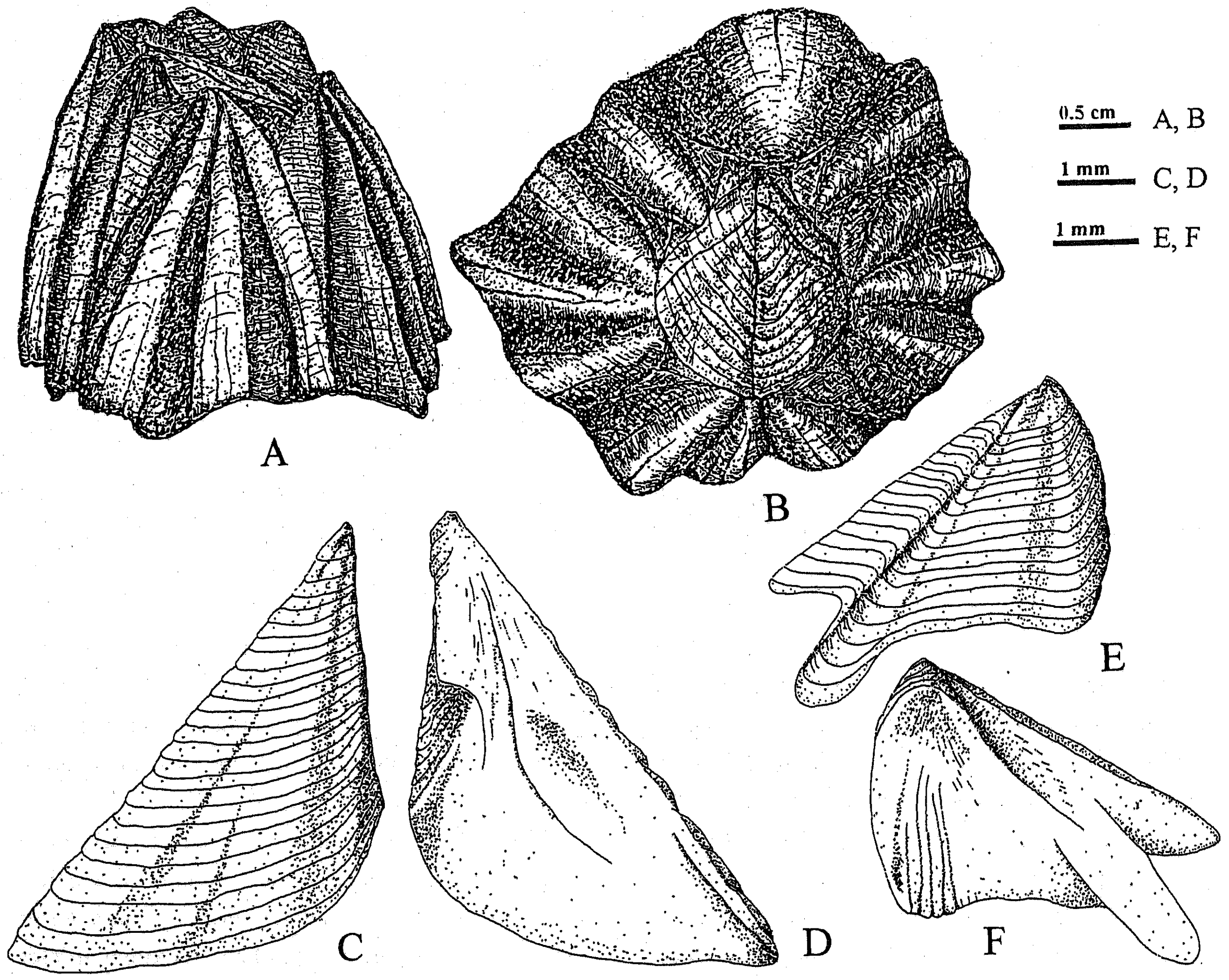

Fig. 1. *Balanus thailandicus* sp. nov., holotype (NMST-Cr13221), shell features. (A) intact specimen, from right side; (B) intact specimen, from above; (C & D) scutum, outer and inner surfaces respectively; (E & F) tergum, outer and inner surfaces respectively.

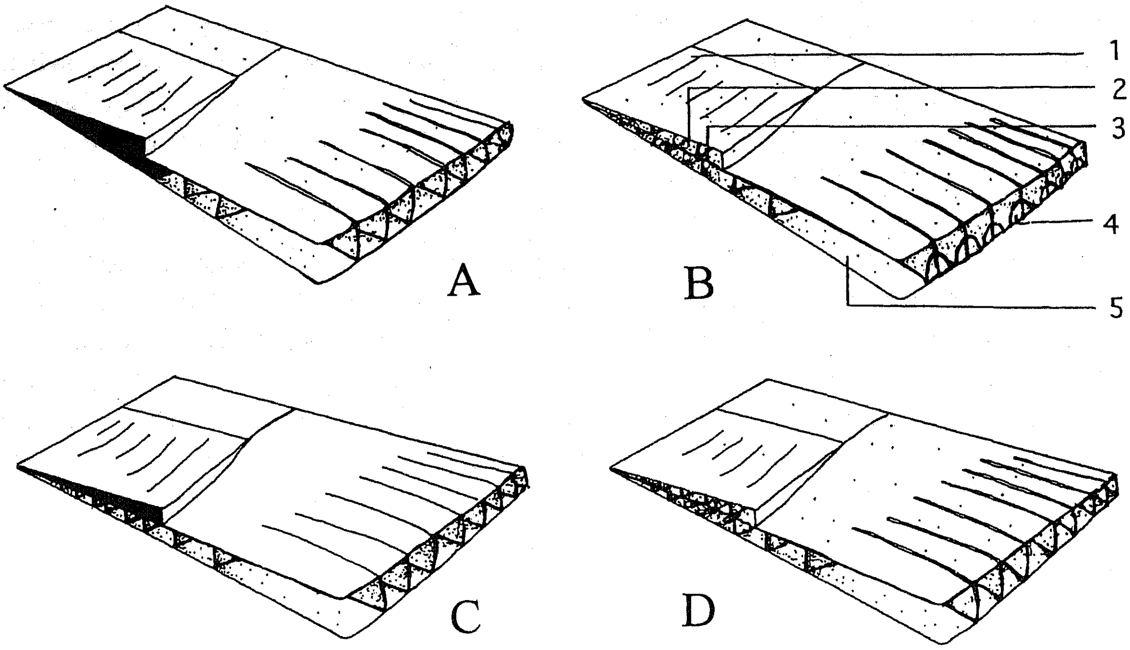

Fig. 2. Schematic view of shell structure. (A) *Balanus thailandicus* sp. nov., (B) *B. patelliformis*, (C) *B. reticulatus*, (D) *B. variegatus*. 1=sheath, 2=inner lamina, 3=transverse septa, 4=longitudinal septa, 5=longitudinal canal of tube.

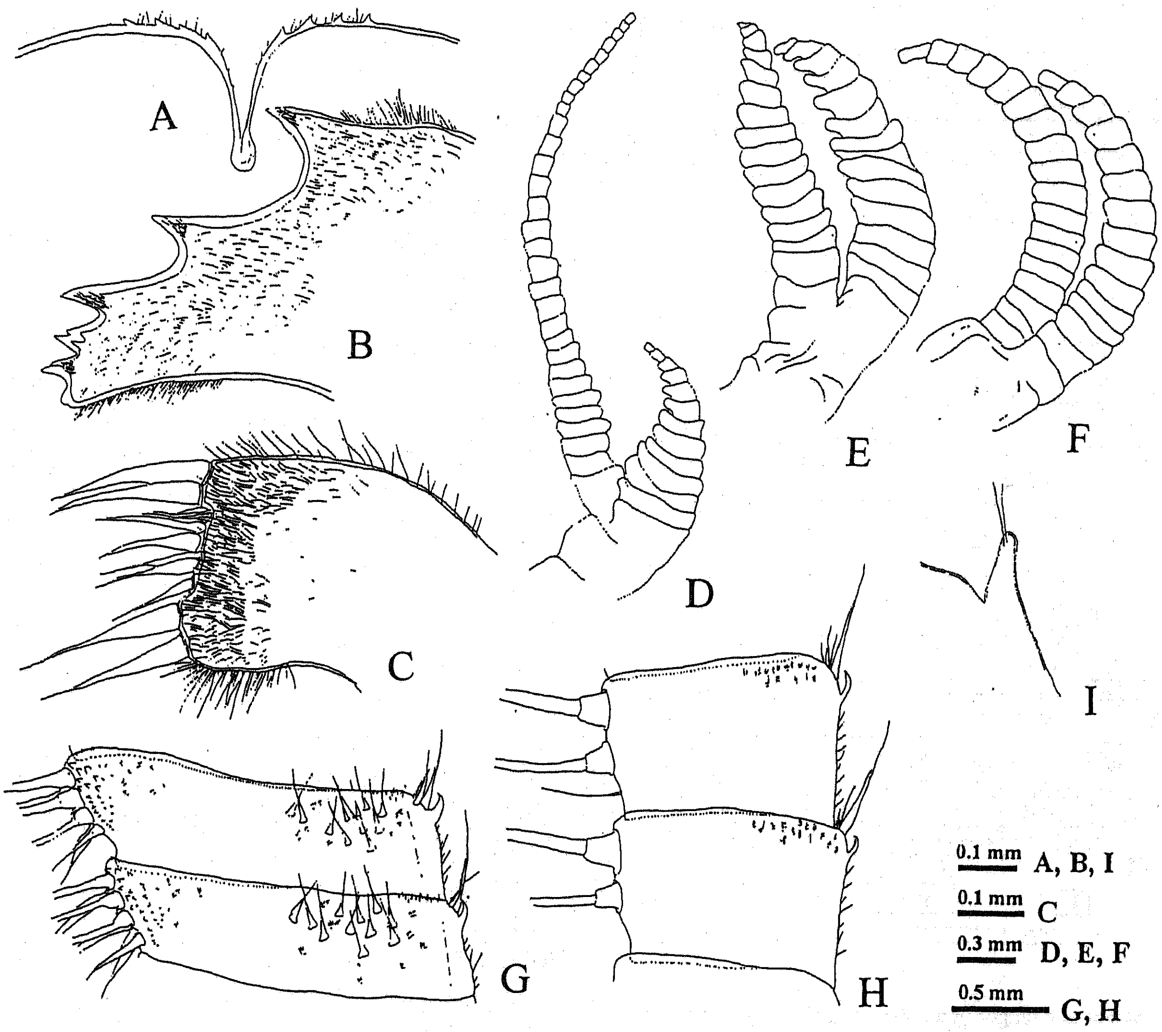

Fig. 3. *Balanus thailandicus* sp. nov., trophi and cirri. (A) labrum; (B) mandible; (C) first maxilla; (D) right cirrus I; (E) right cirrus II; (F) right cirrus III; (G) median articles of anterior ramus of right cirrus III; (H) median articles of anterior ramus of right cirrus IV; (I) basidorsal point of penis. A-C, holotype (NSMT-Cr13221); D-I, 1st Paratype (NSMT-Cr13222); arrows, anterior rami.

posterodistal angle.

Cirri V and VI with a few simple spinules near anterior margins, without conical denticles. Cirrus VI with 3-5 pairs of setae on anterior margins of medial articles of rami.

Penis with a narrow or elongate basidorsal point (Fig. 3I).

Morphological variation

Morphological variation can be seen in the development of the ribs on the exterior of the parietes. The parietes occasionally have a smooth surface without ribs in juveniles. The development of the pit for the lateral depressor muscle in the scutum varies considerably. The arrangement of the mandibular teeth is also subject to considerable variation, particularly concerning the existence of the 4th and 5th teeth.

Affinities

Newman (1982) noted the general characters of the *Balanus amphitrite* complex: small size, smooth or weakly ribbed walls, weakly or unornamented scuta, and being most commonly found in shallow or intertidal brackish environments. All these are also characteristics of *B. thailandicus* sp. nov. While, it is differences from a common members of the complex by the present of large number of articles in the anterior ramus of cirrus I (18-26 articles longer than posterior ramus). Several characteristics of the shell surface, shape of shell, shell structure, tergum, labrum, and cirri show a close relationship between the new species and *B. patelliformis*, *B. reticulatus*, and *B. variegatus* (Bruguière, 1789; Darwin, 1854; Utinomi, 1967; Henry and McLaughlin, 1975; Yamaguchi, 1977) (Table 3). These species all show a macrogeographic sympatric relationship in the

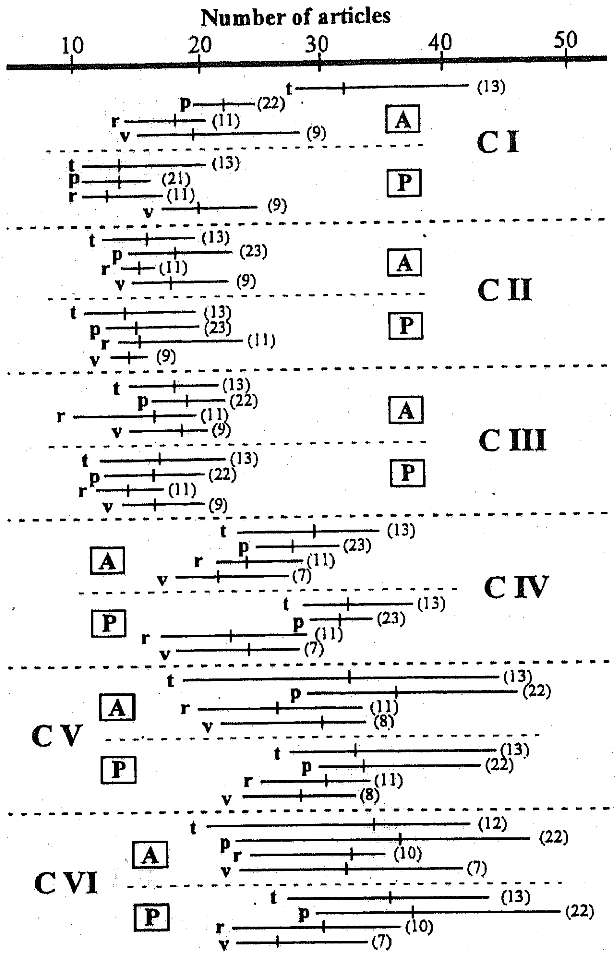

Fig. 4. Means and ranges of numbers of articles in anterior (A) and posterior (P) rami of right cirri of *Balanus thailandicus* sp. nov. (t); *B. patelliformis* (p), *B. reticulatus* (r), and *B. variegatus* (v); (n) = number of individuals examined.

Malay Peninsular and have common characteristics of shell wall structure.

Balanus thailandicus resembles *B. patelliformis* of the *Balanus amphitrite* complex in shell appearance. However, *B. thailandicus* is distinct from *B. patelliformis* in having a solid sheath, erect hooks on the articles of cirri III and IV, a lack of subsidiary tubes in the wall, and a long adductor ridge of the scutum (Puspasari *et al.*, 2000).

Balanus thailandicus is also distinguished from *B. reticulatus* and *B. variegatus* by the development of the ribbed shell walls, the presence of a solid infilling in the upper half of the parietal tubes, the large number of articles in the anterior ramus of cirrus I, and the possession of erect hooks on the rami of cirrus IV. Most characteristics of the new species are shared with *B. reticulatus*, including the solid sheath and the erect hooks on the rami of cirrus III, lack of subsidiary tubes in the wall, the nature of the inner surface of the tergum, and the shape of the basidorsal point of the penis. Therefore, morphological evidence suggests that *B. thailandicus* is closely allied to *B. reticulatus*.

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Table 3. Comparison of some morphological characteristics among certain representatives of the *Balanus amphitrite* complex. *B. patelliformis* from Surat Thani, Thailand (Puspasari et al., 2000); *B. reticulatus* from Gushikawa, Okinawa, Japan; *B. variegatus* from Pak Nakhon, Phanang Bay, Thailand (Puspasari, unpublished data).

Characters	*B. thailandicus* sp. nov.	*B. patelliformis*	*B. reticulatus*	*B. variegatus*
A. Shell				
parietes	ribbed, folded, or smooth	smooth	smooth	smooth
sheath	solid	vesicular	solid	vesicular
parietal tubes	solid in upper half, with transverse septa in lower half	with transverse septa	with transverse septa	with transverse septa
subsidiary tubes	absent	present	absent	absent
radii	transpariental	transpariental	transpariental	transpariental
B. Scutum				
adductor ridge	long	short	short	moderately long
C. Tergum				
spur furrow	open	open	open	open
depressor muscle crests	moderately prominent	very prominent	moderately prominent	moderately prominent
basal margin of carinal side	straight	straight or slightly concave	straight	straight
D. Mouthparts				
maxilla I	with notch	with notch	with notch	without notch
E. Cirrus III				
anterior margin	with conical denticles	with conical denticles	with conical denticles	without conical denticles
erect hooks on posterodistal angles of articles	present	absent	present	absent
F. Cirrus IV erect hooks on posterodistal angles of articles	present	absent	absent	absent
G. Setae	without complex setae	without complex setae	without complex setae	without complex setae
H. Penis				
basidorsal point	naked or with 2 apical setae	naked	naked or with 2 apical setae	with 2 apical setae

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I have checked this proof.
I have marked all changes or
corrections I wish to be made.
Signed Toshi Yamaguchi
Telephone +81-43-290-2832

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NEW RECORD OF *BALANUS ZHUJIANGENSIS* (CIRRIPEDIA, BALANIDAE) FROM OKINAWA, JAPAN

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ABSTRACT

The intertidal barnacle *Balanus zhujiangensis* Ren, 1989, is reported from Okinawa, Japan for the first time. A supplementary description of this species is provided, and the specimens are compared to those from the Zhujiang River estuary which empties into the South China Sea. Several morphological characteristics of the shell, mouthparts, and armature of cirrus III suggest that *B. zhujiangensis* is related to the *B. amphitrite* complex rather than to *B. trigonus* by consistently having but a single row of pits on the external surface of the scutum and lacking an adductor ridge. The presence of scutal pits is interpreted as a means of fascilitating the transmission of light through the valve thereby allowing the photoreceptors to detect changes in light intensity while the operculum is closed.

Balanus zhujiangensis was described by Ren (1989: 467) based on specimens from the estuary of the Zhujiang River in southern China. Ren (1989) contended that *B. zhujiangensis* resembled *B. concavus* Bronn, 1831, especially *B. concavus indica* Nilsson-Cantell, 1932, in external features and in the shape of the tergum. He also pointed out the resemblance to *B. trigonus* Darwin, 1854, because the external surface of the scutum similarly has a row of longitudinal pits. Since first described there have been no subsequent reports of this species, although it has been cited in faunal lists (Huang, 1994; Jones *et al.*, 2000).

Based on two specimens that were collected from Gushikawa, Okinawa, Japan, *B. zhujiangensis* is redescribed and compared with the original description of Ren (1989). The Okinawa specimens as well as those of Ren do not appear to be related to species of *B. concavus* or to *B. trigonus* as originally thought by Ren (1989). Indeed, it appears to be more closely related to some species of the *B. amphitrite* complex. The *B. amphitrite* complex is characterized largely by wall structures such as the parietal tubes and sheath, and by the armature of cirrus III (Henry and McLaughlin, 1975; Puspasari, 2001; Puspasari *et al.*, 2001). The wall structure, opercular plates, trophi, and thoracopods of the present specimens are compared to those described and illustrated by Ren and several species of the *B. amphitrite* complex.

MATERIALS AND METHODS

Two specimens of *B. zhujiangensis* were collected from a test plate (30 × 30 cm) placed at a depth of 1 m for 14 months (July 1997 to September 1998) by a buoy near the Gushikawa (26°22.5'N, 127°52.8'E), Okinawa Island, Japan. The collecting site is near a pier for ships. It faces the open Pacific coast of Okinawa Island. These specimens were associated with *B. amphitrite* Darwin, 1854, and *B. reticulatus* Utinomi, 1967. The open-coast barnacles *Tetraclita squamosa* Bruguière, 1789, *T. formosana* Hiro, 1939, *Yamaguchiella coerulescens* (Spengler, 1790), *Tesseropora* sp., and *Chthamalus* spp. occur at the surrounding intertidal zone of this locality. Ren's (1989) specimens, also collected from a buoy, were from an estuary of the Zhujiang River, southern China. This type of environment is quite different than that occurring at Okinawa.

The smaller specimen examined in this study is 7.6 mm (rostrocarinal diameter) by 7.4 mm (lateral diameter), height 3.5 mm (PCU-BA0082) and the larger 9.1 by 8.4 mm, height 4.2 mm (NSMT-Cr 14163). The holotype of Ren's specimen (Z3-4-3) is 16.2 by 15.0 mm, height 11.5 mm, and the paratype (Z3-4-3-(2)) is 8.0 by 16.3 mm, height 11.0 mm (Ren, 1989). Specimens examined here are deposited in the National Science Museum, Tokyo, Japan (NSMT). Morphological terms of Henry and McLaughlin (1975) and Newman and Ross (1976) are adopted here.

SYSTEMATICS

Family Balanidae Leach, 1817

Genus *Balanus* Da Costa, 1778

Balanus amphitrite complex Henry and McLaughlin, 1975

Balanus zhujiangensis Ren, 1989

Figs. 1A–G, 2A–H

Diagnosis.—Wall conical. Parietes smooth externally, and white or dull rose with longitudinal stripes of lilac, not cross-hatched by transverse striations. Radii wide with slightly oblique summits. Orifice rhomboïdal, toothed. Cavity between sheath and inner lamina filled with calcareous matter. Parietal tubes lacking transverse septa and subsidiary tubes. Exterior of scutum with single row of pits extending down center of valve. Interior lacking adductor ridge. Tergum with carinal margin convex; spur furrow open and broadly rounded distally, basal margin straight on both sides of spur. Labrum with 3 to 4 teeth on each side of deep medial notch. Cirrus III without complex setae. Cirri III–VI with erect hooks around posterior angle.

Supplementary Description.—Wall conical with smooth surface (Fig. 1A, B). Parietes white or dull rose with longitudinal stripes of lilac, not crossed by horizontal striations. Orifice serrated, width more than one-half diameter of rostrocarinal axis. Radii white, wide, summits slightly oblique, and having distinct transverse striations. Alae tinged with dark purple, summits oblique. Cavity between sheath and inner lamina filled in with calcareous material (Fig. 1G). Inner lamina ribbed below, denticulate basally. Parietal tubes in single row, without transverse septa. Basis thin, with radial tubes extending nearly to periphery.

Opercular Plates.—Scutum (Fig. 1C) trigonal, higher than wide; occludent margin toothed; tergal margin straight; basitergal angle obliquely truncated; growth ridges well developed, raised; exterior with single row of pits extending down middle of valve; without longitudinal striations. Scutum (Fig. 1D) smooth on inner surface; articular ridge narrow, slightly longer than one-half length of tergal margin, bluntly or sharply pointed at distal end; articular furrow shallow; pit for adductor muscle distinct; adductor ridge lacking; pit for lateral depressor muscle moderately deep; purplish with narrow white band along tergal margin on external surface, and grayish lavender with white on tergal segment of internal surface. Tergum (Fig. 1E) with articular margin raised; growth ridges distinct; carinal margin slightly convex; spur furrow open and moderately deep; basal margin nearly straight on both sides of spur; spur separated from basiscutal angle by about one-half its own width; articular ridge long and reflexed in upper part (Fig. 1F); articular furrow shallow; crests for depressor muscles moderately long with 4 or 5 insertion sites; external mostly purple with white spur furrow on outer surface, and purple inner surface, except for white spur margins, articular ridge, and crests of depressor muscle.

Mouthparts.—Crest of labrum with numerous setules and 3 to 4 teeth on each side of deep medial notch (Fig. 2A). Mandible with 5 teeth and spinose inferior angle, fifth tooth united with pectinated inferior angle (Fig. 2B). Palps elongate, profusely setose, with short finely pinnate setae on upper margin and also in oblique row near inferodistal angle (Fig. 2C). First maxilla without notch below upper pair of spines, with 8 spines between upper and lower pairs, and with few short spines on inferior angle (Fig. 2D). Second maxilla bilobed, distal lobe oval, large, and strongly setose, while spherical in lower half (Fig. 2E).

Cirri.—Cirrus I with unequal rami, anterior ramus 5–8 articles longer than posterior; long setae at distal sutures of rami and with many spinules on most articles of anterior ramus and on few distal articles of posterior ramus. Cirrus II with anterior ramus 2–4 articles longer than posterior, and with simple spinules near anterior margin. Cirrus III with anterior ramus one article longer than posterior; distal suture of rami with short setae, spinules and conical denticles (= conical teeth of Henry and McLaughlin (1975) that are not true teeth) on outer face near anterior margins (Fig. 2F); with tuft of short setae on distal angles of posterior margins of rami and with erect hooks (= erect teeth of Henry and McLaughlin (1975) that are not true teeth) below posterodistal angles; with pinnate and pectinate setae on the inner face near posterior margins. Cirri IV and V with numerous small conic denticles at anterior margins of proximal articles. Cirri IV–VI with erect hooks below posterior angles of distal articles of rami (Fig. 2G). Cirrus VI with 4 or 5 pairs of setae on anterior intermediate articles. Penis (Fig. 2H) light yellowish turning brown at base, shorter than cirrus VI; clothed with several fine setae from two-third of its length to distolateral edge; two subapical setae present on basidorsal point.

Remarks.—The Okinawa specimens examined in this study (Figs. 1, 2) agree, in general, with the hard parts and appendages de-

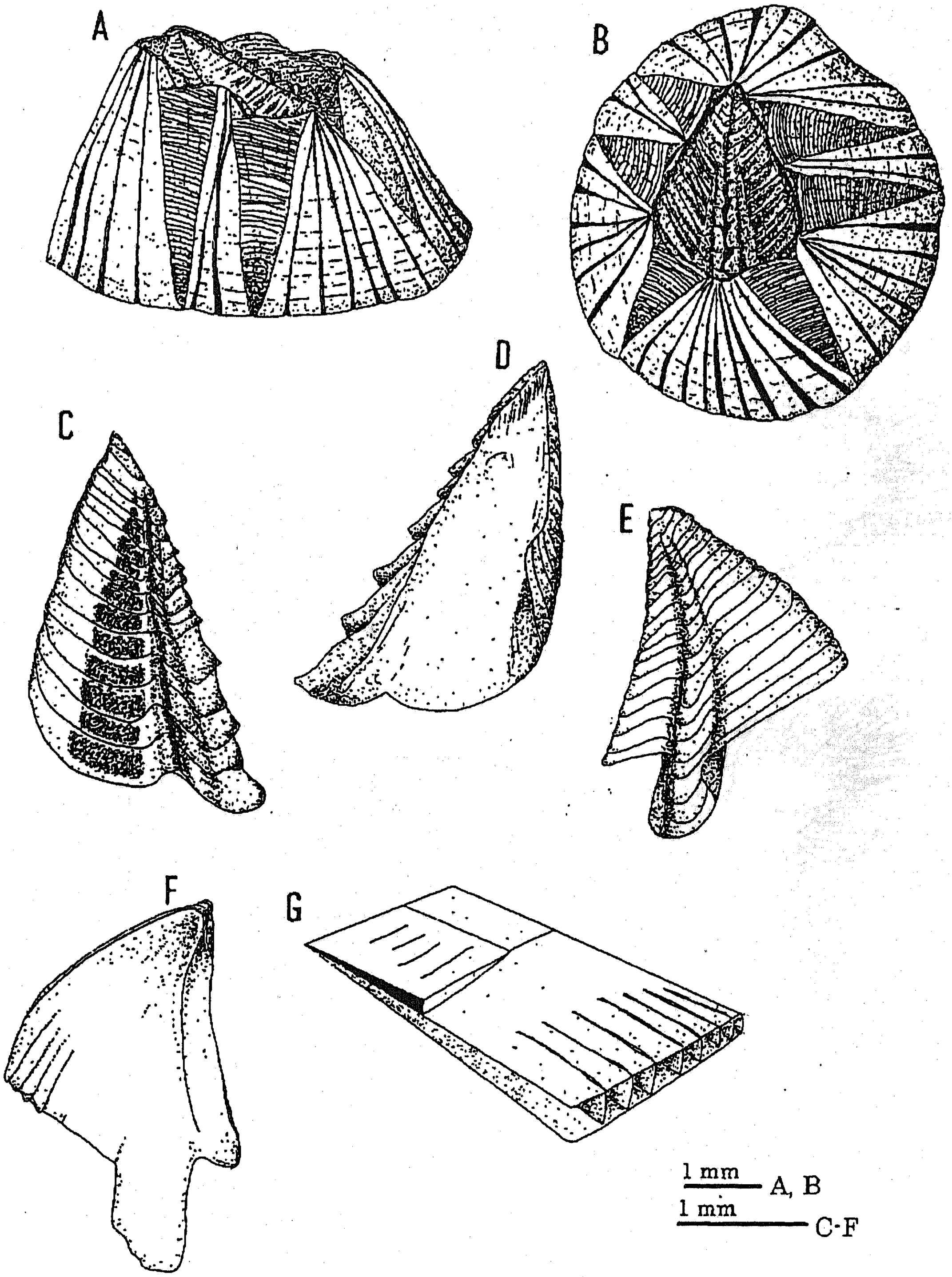

Fig. 1. *Balanus zhujiangensis* Ren (NSMT-Cr 14163) from Gushikawa, Okinawa, Japan. A–B, whole wall; C–D, left scutum, exterior and interior views; E–F, right tergum, exterior and interior views; G, schematic profile of wall structure.

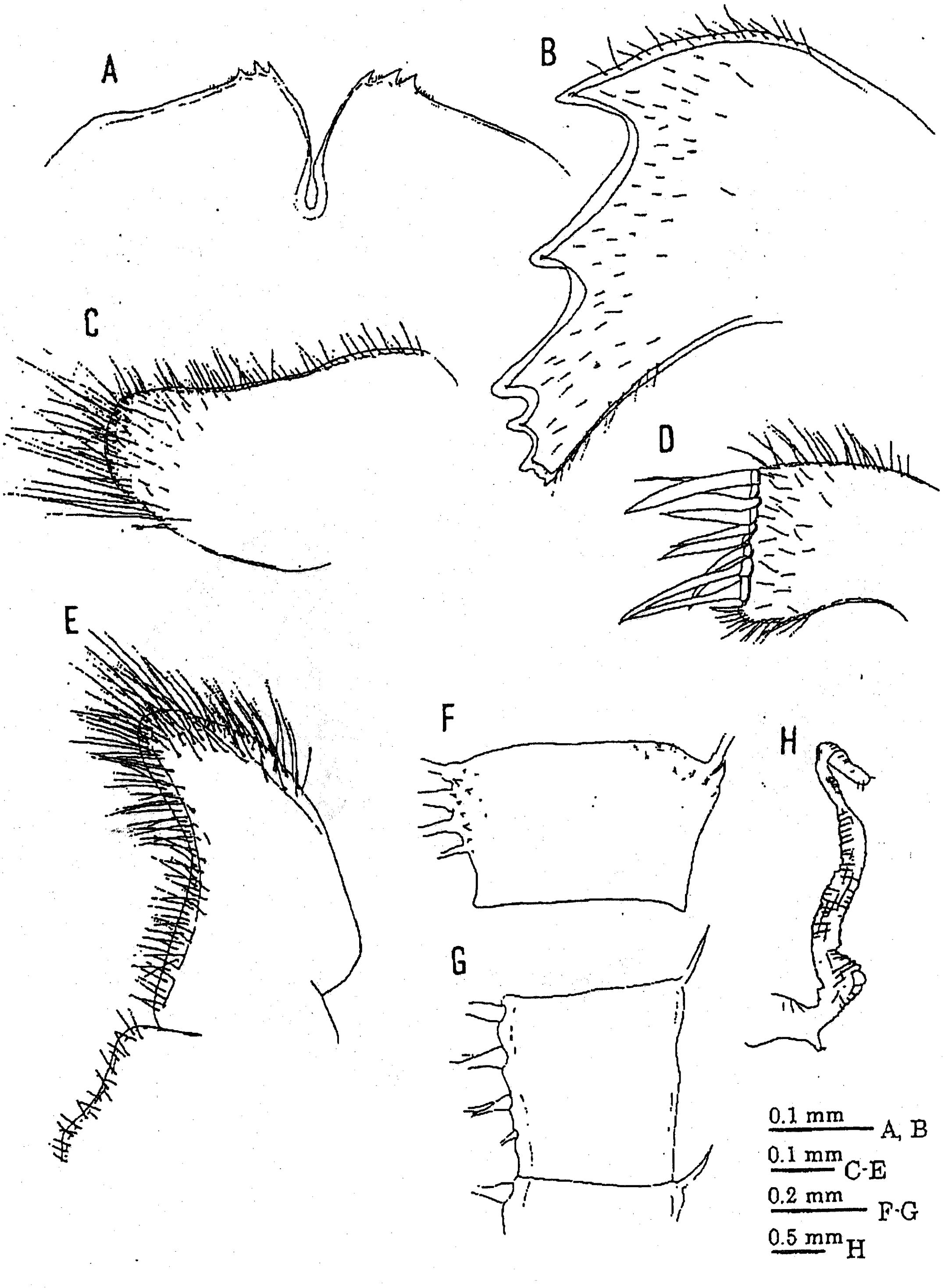

Fig. 2. *Balanus zhujiangensis* Ren (NSMT-Cr 14163) from Gushikawa, Okinawa, Japan. A, labrum; B, right mandible; C, right palp; D, right first maxilla; E, right second maxilla; F, median article of anterior ramus of right cirrus III; G, distal articles of anterior ramus of right cirrus IV; H, penis.

Table 1. Comparison of some morphological characteristics among certain representatives of the *Balanus amphitrite* complex. *Balanus patelliformis* from Surat Thani, Thailand (Puspasari *et al.*, 2000); *B. reticulatus* from Gushikawa, Okinawa, Japan; *B. variegatus* from Pak Nakhon, Phanang Bay, Thailand (Puspasari, unplublished data).

Characters	*B. zhujiangensis*	*B. thailandicus*	*B. reticulatus*	*B. variegatus*
A. Shell				
transversal stripes	absent	absent	present	present
sheath	solid	solid	solid	vesicular
parietal tubes	absent transverse septa	solid in upper half, with transverse septa in lower half	with transverse septa	with transverse septa
subsidiary tubes	absent	absent	absent	absent
radii	transparietal	transparietal	transparietal	transparietal
B. Scutum				
adductor ridge	absent	long	short	moderately long
C. Tergum				
spur furrow	close	open	close	close
depressor muscle crests	moderately prominent	moderately prominent	moderately prominent	moderately prominent
basal margin of carinal side	straight	straight	straight	straight
D. Mouthparts				
labrum	simple denticulate	simple denticulate	simple denticulate	simple denticulate
maxilla I	without notch	with notch	with notch	without notch
E. Cirrus III				
anterior margin	with conical denticles	with conical denticles	with conical denticles	without conical denticles
erect hooks on posterodistal angles of articles	present	present	present	absent
F. Cirrus IV				
erect hooks on posterodistal angles of articles	present	present	absent	absent
G. Setae	without complex setae	without complex setae	without complex setae	without complex setae
H. Penis				
basidorsal point	with 2 apical setae	naked or with 2 apical setae	naked or with 2 apical setae	with 2 apical setae

scribed by Ren (1989) except for the tergum and first maxilla. The tergum of the Okinawa specimens has four to five crests for the lateral depressor muscle, whereas Ren's specimens do not have any crests. We have discounted the possibility that this is due to size (age) because crests are present even in young stages of species in the *B. amphitrite* complex. The first maxilla has eight small spines between the major upper pair of spines and single lower spine, whereas Ren's specimens have 16 intermediate spines.

DISCUSSION AND CONCLUSION

Newman (1982) noted that in general the barnacles within the *Balanus amphitrite* complex have a relatively small shell with smooth or weakly ribbed walls, weakly developed scuta, and commonly inhabits shallow or intertidal brackish environments. Puspasari *et al.* (2001) and Puspasari (2001) summarized several diagnostic characteristics of the *B. amphitrite* complex including the structures between the sheath and inner lamina, parietal tubes, and armature of the thoracopods. These morphological characteristics are common with those of *B. zhujiangensis*, except for the presence of a row of pits on the external surface of the scutum and the absence of an adductor ridge on the scutum.

The characteristic solid sheath, lack of subsidiary tubes, shape of tergum, and armature of cirri III and IV of *B. zhujiangensis* show a close relationship with *B. variegatus* Darwin, 1854, *B. reticulatus* Utinomi (1967), and *B. thailandicus* Puspasari *et al.* (2001) of the *B. amphitrite* complex. *Balanus zhujiangensis* also differs from *B. variegatus* by the characteristics of the shell, cirri III and IV, and from *B. reticulatus* by several characteristics of the shell and first maxilla (Table 1).

Balanus zhujiangensis resembles *B. thai-*

landicus in shell structure, tergum, labrum, presence of erect hooks on cirri III and IV, and basidorsal point of penis. However, it is distinct from *B. thailandicus* in lacking transverse septa in the longitudinal tubes and a notch in the first maxilla (Puspasari *et al.*, 2001).

Most of the characteristics of *B. zhujiangensis* are shared with the three abovementioned members of the *B. amphitrite* complex. Therefore, morphological evidence suggests that *B. zhujiangensis* is most closely allied to *B. variegatus, B. reticulatus,* and *B. thailandicus*.

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The solid sheath, lack of subsidiary tubes, tergum, and armature of cirri III and IV of *B. zhujiangensis* show a close resemblance with *B. trigonus* complex. However, the scutum of *B. trigonus* has up to six rows of relatively small pits, and they are either circular or ovate, whereas in *B. zhujiangensis* there is but ~~a~~ single row, and they are large, rectangular, and occupy one-third or more the width of the plate.

We can find no reference to the functional significance of the pits that develop on the external surface of the scutum of this and several other species, such as *B. trigonus*. Fundamentally the calcareous scuta in balanids are opaque, although some, when cleaned and immersed in water, are only slightly translucent. It is apparent that the scuta are significantly thinner where these pits occur and, when the scuta ~~is~~ candled, light is more readily transmitted through the plate where the pits occur. In balanids the ability to detect changes in light intensity is well known and commonly referred to as the shadow reflex which is mediated by the medial and paired lateral ocelli or photoreceptors, which have no image forming capability. The lateral photoreceptors are located beneath and near the basal margins of the scuta. By virtue of their position it seems reasonable to hypothesize that these pits are thinly paned windows for detecting changes in light intensity thereby obviating the need to open the aperture.

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Geographical Distribution

Balanus zhujiangensis is known from Okinawa Island as well as the type locality bordering the South China Sea (Ren, 1989).

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Genetic relationship among Japanese sentinel crabs (Decapoda: Ocypodidae: genus *Macrophthalmus*)

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Abstract

Seven species (eight populations) of sentinel crabs (genus *Macrophthalmus*) from the Japan coast and *Uca vocans* and *Ocypode ceratophthalma*, were examined electrophoretically for genetic variations in 13 enzymatic and one non-enzymatic protein comprising 17 loci. Most species were highly differentiated from each other (Nei's genetic distance, 0.29–1.63). The least genetic distance was found between *M. japonicus* and *M. banzai*, the genetic distinctiveness of the two taxa being supported by three divergent loci with no common allele. The genetic relationships among *Macrophthalmus* species differed greatly from those inferred from morphological features, with a UPGMA tree suggesting that the sub-genus *Macrophthalmus* is polyphyletic. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Allozyme; Crustacea; *Macrophthalmus*; *Macrophthalmus banzai*; *Macrophthalmus japonicus*; Ocypodid crabs; Phylogeny; Taxonomy

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1. Introduction

Sentinel crabs (genus *Macrophthalmus* Latreille, 1829) inhabit subtidal and tidal flats of various substrata, such as mud, sand, rock, dead coral reef and seagrass, in the temperate to tropical Indo-West Pacific region. The genus currently includes 41 extant species (Barnes, 1977; Serène, 1981; Wada and Sakai, 1989; Takeda and Komai, 1991; Holthuis, 1995; Poupin, 1997) and is classified into seven subgenera (*Hemiplax*, *Macrophthalmus*, *Mareotis*, *Mopsocarcinus*, *Paramareotis*, *Tasmanoplax* and *Venitus*) (Barnes, 1967; Komai et al., 1995). The taxonomy of *Macrophthalmus* was substantially clarified by a series of studies by Barnes (1967, 1971, 1973, 1977), but the phylogenetic relationship has not so far been examined.

Japan is represented by 18 *Macrophthalmus* species (Sakai, 1976; Takeda, 1981; Wada and Sakai, 1989; Takeda and Komai, 1991; Kosuge and Wada, 1992; Kitaura and Wada, 1999). The

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most common of these, *M. japonicus*, for which two forms differing in male waving display and some morphological traits have been described (Wada, 1978), was subsequently considered to include a second species, described as *M. banzai* by Wada and Sakai (1989). Nevertheless, discrimination of the two species among juvenile specimens on the basis of external morphology remained difficult, complicated by the confirmation of incomplete post-mating reproductive isolation between them (Wada, 1989). The present study investigated the genetic relationships of seven common Japanese coastal species of *Macrophthalmus*, including *M. japonicus* and *M. banzai*, utilizing allozyme analysis, a useful tool for examining the degree of genetic divergence between apparently recently-diverged species.

2. Materials and methods

2.1. Samples and electrophoresis

Seven species of *Macrophthalmus* and two species of the sub-family Ocypodinae as comparative materials, used in this study are listed in Table 1, together with collection data and number of individuals examined (see Fig. 1). The specimens were collected by digging in the substrate with a trowel. All samples were transported to the laboratory alive or frozen with dry ice and stored at −80°C. Frozen muscle from the ambulatory legs plus the viscera of each individual were used for starch gel electrophoresis. In the case of *M. boteltobagoe*, the entire body was used for electrophoresis because of their small size. The 17 enzyme systems investigated, following screening for 40 enzymes and buffer systems used, are shown in Table 2. The staining procedures for specific enzymes were similar to those of Shaw and Prasad (1970), Ayala et al. (1972) and Harris and Hopkinson (1976). Alleles at each locus were designated by letters in alphabetical order, starting with the allele encoding the most anodally migrating isozyme.

2.2. Data analysis

From individual genotypes, allele frequencies were determined for all species, and the unbiased genetic distance (*D*) and identity (*I*) calculated

Table 1
List of species studied, with collection locations and number of individuals examined (see Fig. 1)

Species	Locality	No. of individuals	Abbreviations
Sub-family			
Macrophthalminae			
Genus *Macrophthalmus*			
Sub-genus *Macrophthalmus*			
M. (M.) abbreviatus	(1) Wakaura, Wakayama Pref.	16	MABB
M. (M.) convexus	(2) Urauchi River, Iriomote Is., Okinawa Pref.	23	MCON
M. (M.) milloti	(3) Noharazaki, Iriomote Is., Okinawa Pref.	20	MMIL
Sub-genus *Mareotis*			
M. (M.) japonicus	(4) Shirahama, Wakayama Pref.	24	MJAP
M. (M.) banzai	(4) Shirahama, Wakayama Pref.	14	MBAN1
M. (M.) banzai	(5) Ohura, Okinawa Is., Okinawa Pref.	22	MBAN2
M. (M.) definitus	(6) Miyara River, Ishigaki Is., Okinawa Pref.	18	MDEF
Sub-genus *Paramareotis*			
M. (P.) boteltobagoe	(7) Horikawa, Okinawa Is., Okinawa Pref.	24	MBOT
Sub-family *Ocypodinae*			
Genus *Ocypode*			
O. ceratophthalma	(8) Ujidomari, Okinawa Is., Okinawa Pref.	10	OCER
Genus *Uca*			
U. vocans	(9) Senagajima, Okinawa Is., Okinawa Pref.	12	UVOC

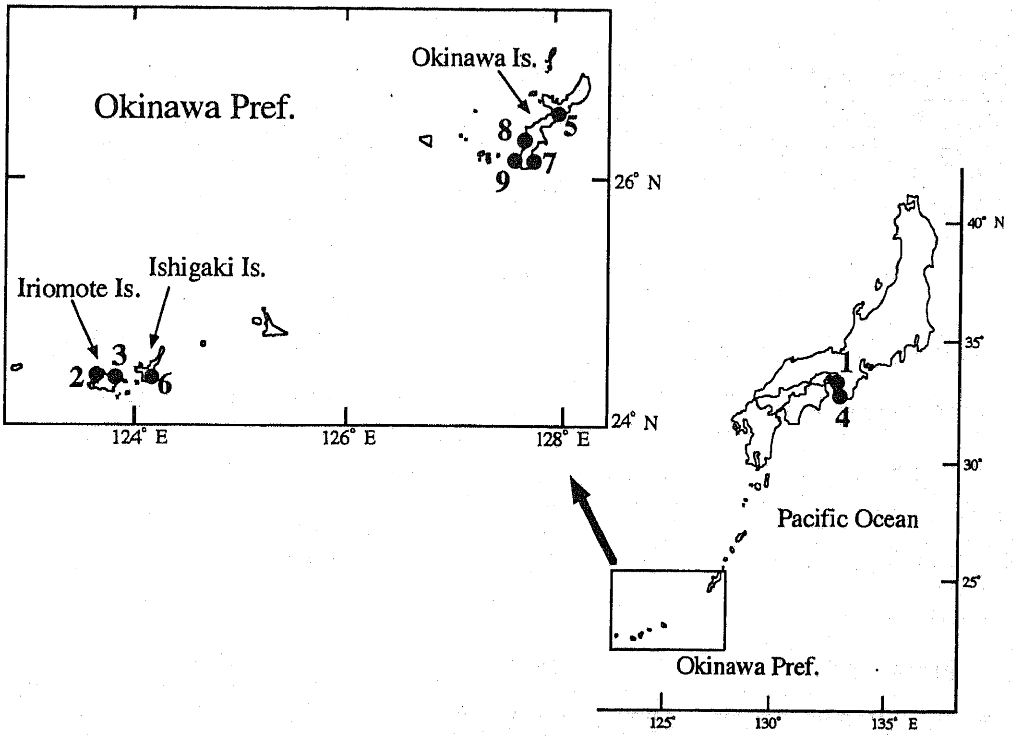

Fig. 1. Collecting locations (1–9) for the species studied. Location names and sample sizes are provided in Table 1.

for the pairwise combinations of all species according to Nei (1978). A dendrogram based on genetic distance was constructed using the unweighted pair group method with arithmetic means (UPGMA) of Sneath and Sokal (1973).

3. Results

Of the 17 loci examined, one (*Dia*-2) was monomorphic among *Macrophthalmus* species, and the remainder polymorphic (Table 3). But within species, six loci (*Aat*-1, *Dia*-1, *Gpi*, *Idh*, *Mdh* and *Pgm*) were polymorphic and the remainder monomorphic. The percentage of polymorphic loci ranged from 5.88 to 17.76, with an average heterozygosity of 0.004–0.051. Nei's unbiased genetic distance values (Nei, 1978) among the seven *Macrophthalmus* species and two ocypodine species, calculated from the allele frequencies of the 17 loci, are given in Table 4. The pairwise genetic distance values among the *Macrophthalmus* species ranged from 0.29 (between *M. japonicus* and *M. banzai*) to 0.84 (between *M. abbreviatus* and *M. convexus*), indicating that all species were substantially diverged from one another.

Between *M. japonicus* and *M. banzai*, no common allele was detected at three out of 17 loci. The two species shared common alleles at the remaining 14 loci, for 12 of which identical alleles were fixed in the two, whereas alleles at the two other loci (*Gpi*, *Idh*) showed highly divergent frequencies. The genetic distance between the species (0.29) was the smallest value among the pairwise distances determined.

The mean genetic distance values among three species of the subgenus *Mareotis* and three of subgenus *Macrophthalmus* were 0.35 and 0.66, respectively. The mean intersubgeneric *D* values were 0.54 between *Macrophthalmus* and *Mareotis*, 0.68 between *Mareotis* and *Paramareotis* and 0.67 between *Macrophthalmus* and *Paramareotis*. *M. boteltobagoe*, included in the subgenus *Paramareotis*, was genetically highly differentiated from other *Macrophthalmus* species. Six divergent loci with no common alleles were observed between *M. boteltobagoe* and other *Macrophthalmus* species, with genetic distances between them ranging from 0.61 to 0.76.

The genetic relationships among the seven *Macrophthalmus* species examined is presented in Fig. 2. This tree does not reflect the present

Table 2
Enzymes and loci examined, and tissue and buffer systems used for electrophoresis

Enzyme (abbreviation, EC number)	Locus	Tissue	Buffer system[a]
Aldolase (ALD, 4.1.2.13)	*Ald*	Muscle	TC7.0
Aspartate aminotransferase (AAT, 2.6.1.1)	*Aat-1*	Muscle	CAPM, CAPM7.0
	Aat-2	Muscle	CAPM, CAPM7.0
Diaphorase (DIA, 1.6.2.2)	*Dia-1*	Viscera	TBE, LiOH
	Dia-2	Viscera	TBE, LiOH
	Dia-3	Muscle	TBE, LiOH
Esterase (EST, 3.1.1.1)	*Est*	Viscera	TCE, CAPM
Glucose-6-phosphate isomerase (GPI, 5.3.1.9)	*Gpi*	Muscle	TC8.0, LiOH
Glyceraldehyde-3-phosphate dehydrogenase (GPDH, 1.2.1.12)	*Gpdh*	Muscle	TC7.0, TCE
Glycerol-3-phosphate dehydrogenase (G3PDH, 1.1.1.8)	*G3pdh*	Muscle	CAPM7.0, TC7.0
Hexokinase (HK, 2.7.1.1)	*Hk*	Muscle	TBE
Isocitrate dehydrogenase (IDH, 1.1.1.42)	*Idh*	Muscle	TC8.0
Malate dehydrogenase (MDH-2, 1.1.1.37)	*Mdh*	Muscle	TC7.0, CAPM7.0
Peptidase (PEP (Lv), 3.4.11)	*Pep (Lv)*	Viscera	
Phosphoglucomutase (PGM, 5.4.2.2)	*Pgm*	Muscle	TC8.0
General protein (GP)	*Gp*	Muscle	CAPM, TC7.0, TCE

[a] *Abbreviations:* TC7.0: Tris-citric acid, pH 7.0 (Shaw and Prasad, 1970); TC8.0: Tris-citric acid, pH 8.0 (Shaw and Prasad, 1970); CAPM: Citric acid-aminopropyl morpholine, pH 6.1 (Clayton and Tretiak, 1972); CAPM7.0: Citric acid-aminopropyl morpholine, pH 7.0 (Clayton and Tretiak, 1972); TBE: Tris-borate-EDTA, pH 8.7 (Boyer et al., 1963); LiOH: Lithium hydroxide, pH 8.1/8.5 (Selander et al., 1971); TCE: Tris-citric acid-EDTA, pH 7.0 (Ayala et al., 1972).

subgeneric classification. The allozyme data suggests two distinct lineages in the genus *Macrophthalmus*, with species of subgenus *Macrophthalmus* falling into both, making this subgenus polyphyletic.

4. Discussion

4.1. Genetic variability in sentinel crab species

The expected average heterozygosity in the present study ranged from 0.004 to 0.051 (Table 3), low values compared with that given for invertebrates general (0.15) by Powell (1975), but similar to those of other ocypodid crabs (e.g., 0.038–0.045 in *Macrophthalmus hirtipes* (Sin and Jones, 1983), 0.012 in *Ocypode quadrata* and 0.046 in *Ocypode occidentalis* (Nelson and Hedgecock, 1980), 0–0.11 in Malaysian fiddler crabs of *Uca* (Suzawa et al., 1993). Low genetic variability in decapod crustaceans has also been reported (e.g. Gooch, 1977; Turner and Lyerla, 1980; Hedgecock et al., 1982). The early suggestion by Gooch (1977) that this is a characteristic of decapods is further supported by the present results. Some studies have suggested that the low genetic variability in crustacean species in fact reflects low rates of mutation or intracistronic recombination (Nemeth and Tracey, 1979) and their mobility (Hedgecock et al., 1982).

4.2. Genetic relationships between M. japonicus and M. banzai

In the present study, Nei's measure of genetic identity between *M. japonicus* and *M. banzai* was 0.75, corresponding to a genetic distance of 0.29. Hedgecock et al. (1982) established the mean genetic identity for congeneric crustacean species as 0.59 ± 0.17, following 40 comparisons between various crustacean species. The genetic identity value between *M. japonicus* and *M. banzai* is somewhat higher but similar to the average value between decapod crustacean species. Notwithstanding the relatively higher value of the genetic identity, on the basis of the observation of three divergent loci with no common allele between them, *M. japonicus* and *M. banzai* are considered to be genetically-distinct, but recently divergent, species.

Table 3
Allele frequencies, expressed as percentages, at 17 genetic loci in seven species of Macrophthalminae and two species of Ocypodinae

Locus	Allele	Species examined and allele frequency									
		MABB	MCON	MMIL	MJAP	MBAN1	MBAN2	MDEF	MBOT	OCER	UVOC
Aat-1	*a*	0.940									
	b	0.060	1.000	1.000	1.000	1.000	1.000	1.000			1.000
	c									1.000	
	d								1.000		
		(16)	(15)	(13)	(16)	(9)	(9)	(9)	(8)	(10)	(11)
Aat-2	*a*		1.000	1.000						1.000	
	b								1.000		
	c	1.000			1.000						
	d					1.000	1.000	1.000			
	e										1.000
		(10)	(11)	(7)	(12)	(9)	(8)	(8)	(10)	(10)	(9)
Ald	*a*										1.000
	b		1.000	1.000				1.000			
	c	1.000			1.000	1.000	1.000		1.000	1.000	
		(10)	(10)	(10)	(8)	(7)	(6)	(5)	(2)	(5)	(3)
Dia-1	*a*	1.000	0.960	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b		0.040								
		(16)	(13)	(14)	(14)	(10)	(8)	(14)	(13)	(10)	(12)
Dia-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		(15)	(8)	(7)	(14)	(7)	(6)	(12)	(13)	(6)	(12)
Dia-3	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
	b									1.000	
		(10)	(9)	(5)	(8)	(2)	(6)	(3)	(4)	(7)	(4)
Est	*a*				1.000						1.000
	b	1.000	1.000			1.000	1.000	1.000	1.000		
	c			1.00						1.000	
		(15)	(15)	(16)	(16)	(10)	(14)	(14)	(16)	(10)	(4)
Gpdh	*a*		1.000	1.000	1.000	1.000	1.000	1.000	1.000		
	b	1.000									1.000
	c									1.000	
		(16)	(19)	(18)	(20)	(9)	(13)	(8)	(9)	(10)	(12)
G3pdh	*a*		1.000	1.000							1.000
	b										
	c	1.000			1.000	1.000	1.000	1.000	1.000	1.000	
		(12)	(19)	(15)	(15)	(11)	(10)	(10)	(7)	(8)	(9)
Gpi	*a*	0.900		0.900	0.063	0.083	0.300		1.000	1.000	
	b	0.100	1.000	0.100	0.937	0.250	0.200	0.938			1.000
	c					0.667	0.500	0.062			
		(10)	(10)	(10)	(8)	(6)	(5)	(8)	(6)	(8)	(4)
Hk	*a*			1.000	1.000	1.000	1.000	1.000			
	b	1.000	1.000						1.000		1.000
	c									1.000	
		(13)	(10)	(10)	(12)	(7)	(6)	(12)	(9)	(8)	(10)
Idh	*a*										0.111
	b		1.000		1.000	0.180	0.071	1.000	1.000	0.312	0.888
	c	1.000		1.000		0.820	0.857			0.687	
	d						0.071				
		(11)	(14)	(12)	(12)	(11)	(7)	(15)	(9)	(8)	(9)
Mdh	*a*									0.875	
	b	0.094	1.000	0.875	1.000	1.000	1.000	1.000	1.000		1.000
	c	0.906		0.125						0.125	
		(16)	(17)	(16)	(16)	(12)	(8)	(18)	(10)	(10)	(12)
Mpi	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
	b									1.000	1.000
		(10)	(13)	(11)	(12)	(10)	(9)	(11)	(11)	(6)	(8)

Table 3 (*Continued*)

Locus	Allele	Species examined and allele frequency									
		MABB	MCON	MMIL	MJAP	MBAN1	MBAN2	MDEF	MBOT	OCER	UVOC
Pep (Lv)	*a*							1.000			
	b			1.000						1.000	
	c		1.000			1.000	1.000				
	d				1.000						1.000
	e								1.000		
	f	1.000									
		(12)	(10)	(10)	(12)	(9)	(8)	(10)	(8)	(6)	(8)
Pgm	*a*								0.200		
	b								0.800		
	c	1.000	1.000	0.937	1.000	1.000	1.000				
	d			0.062				1.000			
	e									1.000	1.000
		(11)	(8)	(8)	(9)	(8)	(7)	(8)	(10)	(8)	(8)
Gp	*a*	1.000		1.000				1.000	1.000	1.000	1.000
	b		1.000		1.000	1.000	1.000				
		(16)	(16)	(14)	(15)	(12)	(11)	(13)	(13)	(10)	(12)
Percentage of loci polymorphic[a]		17.65	5.88	17.65	5.88	11.76	11.76	5.88	5.88	11.76	5.88
Mean number of alleles per locus		1.18	1.06	1.18	1.06	1.18	1.24	1.06	1.06	1.12	1.06
Average heterozygosity (Expected)		0.027	0.004	0.030	0.007	0.046	0.051	0.007	0.019	0.035	0.012

[a] *P* = criterion for polymorphism below 0.99 for major allele frequency.

See Table 1 for abbreviations of species. Number of individuals examined shown in parentheses.

Table 4
Nei (1978) unbiased genetic distances (below diagonal) and genetic identities (above diagonal) among seven species of Macrophthalminae and two species of Ocypodinae

	Subgen. *Macrophthalmus*			Subgen. *Mareotis*				Subgen. *Paramaeotis*		
	MABB	MCON	MMIL	MJAP	MBAN1	MBAN2	MDEF	MBOT	OCER	UVOC
MABB		0.432	0.486	0.498	0.556	0.572	0.434	0.542	0.409	0.376
MCON	0.840		0.652	0.645	0.689	0.682	0.645	0.534	0.197	0.525
MMIL	0.721	0.428		0.538	0.597	0.613	0.602	0.469	0.463	0.420
MJAP	0.698	0.439	0.620		0.752	0.746	0.645	0.481	0.263	0.524
MBAN1	0.588	0.373	0.516	0.285		1.000	0.694	0.504	0.289	0.329
MBAN2	0.559	0.383	0.489	0.293	0.000		0.686	0.512	0.303	0.321
MDEF	0.834	0.439	0.508	0.439	0.365	0.376		0.537	0.260	0.465
MBOT	0.612	0.628	0.756	0.732	0.686	0.669	0.622		0.322	0.412
OCER	0.894	1.626	0.769	1.335	1.241	1.193	1.349	1.134		0.318
UVOC	0.979	0.644	0.869	0.646	1.113	1.137	0.766	0.887	1.144	

See Table 1 for the abbreviations for species.

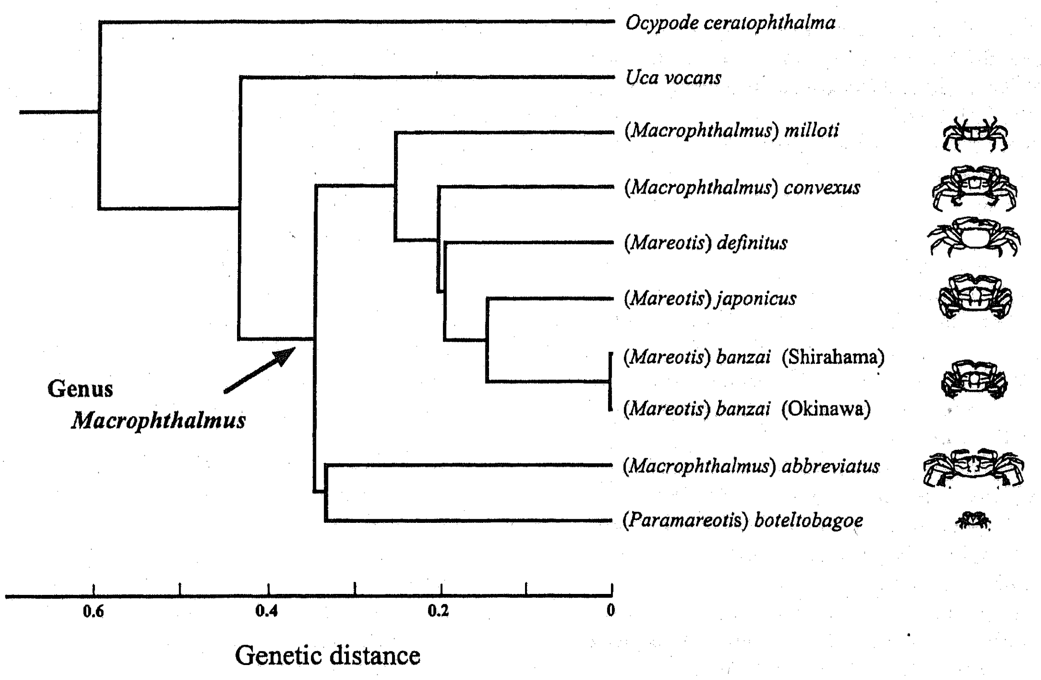

Fig. 2. UPGMA dendrogram of seven species of Japanese sentinel crabs and two ocypodine species based on Nei's genetic distance. Species of the genus *Macrophthalmus* are represented by sub-generic and specific names.

4.3. Phylogenetic implications

The genetic relationships among the subgenera of genus *Macrophthalmus* (Fig. 2) differed greatly from their relationships inferred from morphological features. The dendrogram comprised two main groups, one including a species of the subgenus *Paramareotis* plus *M. abbreviatus* of the subgenus *Macrophthalmus* and the other subgenus *Mareotis* plus *M. convexus* and *M. milloti*, both of the subgenus *Macrophthalmus*. The finding that the subgenus *Macrophthalmus* is apparently polyphyletic suggests that some morphological features used to characterize that subgenus, such as epistome shape and ratio of carapace width to length, do not reflect a phylogenetic relationship, but have in fact resulted from complex evolutionary processes, such as convergence or parallelism. In contrast, the species of the subgenus *Mareotis* formed a cluster, suggesting the subgenus is monophyletic (Fig. 2). However, this study included only seven of 41 species of genus *Macrophthalmus*, representing three of the seven subgenera. Further studies, including a broad representation of all subgenera of *Macrophthalmus*, are needed to clarify the overall phylogenetic relationships of the *Macrophthalmus* species.

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