Evolution and paleobiogeography of Late Triassic bivalve Monotis from Japan

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ABSTRACT: A Late Triassic bivalve genus, Monotis occurs in 22 local areas in Japan. Japanese Monotis is composed of four species and a subspecies, each of which shows a considerably wide range of intraspecific variation; i.e. M. scutiformis, M. ochotica densistriata, M. ochotica ochotica, M. zabaikalica and M. mabara occur in upward sequence. The successive occurrence of these forms except M. mabara, constitutes four Monotis zones, which can be recognized throughout Japan. The last species, M. mabara is associated with M. zabaikalica in the upper part of the M. zabaikalica Zone. The lineage from M. scuti-formis to M. ochotica ochotica through M. ochotica densistriata, shows gradual decrease of the number of primary radial plicae. The evolutionary trend can be regarded as paedo-morphic. Two distinct lineages seem to have originated from M. ochotica ochotica. One is M. zabaikalica, which is probably of direct descent and is characterized by the acceler-ated (or peramorphic) disappearance of radial plicae. The other species, M. mabara, appears to have been a subordinate branch and shows increase of the number of radial plicae. Japanese Monotis beds are generally characterized by coarse-grained clastic sedi-ments indicating some shallow marine environment. This suggests that the habitat of these Japanese species must have been considerably different from that of M. salinaria which occurs from the Hallstatt Limestone facies of the Tethyan province. Japanese Monotis fauna may belong to the same faunal province as that of east Siberia. But quite different Late Triassic bivalve faunas, which bear some obvious Tethyan elements, occur in the Sambosan Belt of the Outer Zone of southwest Japan.

1 INTRODUCTION

In Mesozoic times, several characteristic thin-shelled extinct bivalved genera, such as Daonella, Halobia, Monotis, Bositra, Buchia and Inoceramus, are known. They are useful for biostratigraphy because of their world-wide geographic distribution and short stratigraphic range. They are also noticeable for their peculiar morphology and unique mode of fossil occurrence. Furthermore, they are important for evolu-tionary studies because they show rapid morphological change with time. The bio-geographical significance of these bival-ves has also increased with development of plate tectonics theory. Many problems con-cerning their ecology and evolution, how-ever, remain unsolved.

Among others, Late Triassic Monotis is found in abundance from 22 local areas in Japan and seems to offer excellent materi-al for evolutionary studies (Fig.1). It

occurs from only a part of the Norian or the Norian-Rhaetian, in which ammonoids and other index fossils are comparatively rare (Tozer 1979, 1980). Tozer (1980) con-cluded that Monotis occurs only from two ammonite zones, i.e. M. scutiformis from the Himavatites columbianus Zone, and M. ochotica, M. salinaria and M. subcircularis from the Gnomohalorites cordilleranus Zone. Considering Harland et al.'s (1982) age determination, the absolute time range of Monotis can be estimated to be only about a few to several million years.

In this paper, at first, the taxonomic problems of Monotis are reviewed, because Monotis taxonomy is the basic data for fur-ther implications. Next, the chronological and evolutionary changes of Japanese Mono-tis are presented based on stratigraphical Monotis sequences throughout Japan. Then, the paleobiogeography of Monotis is men-tioned with special reference to the Tethys.
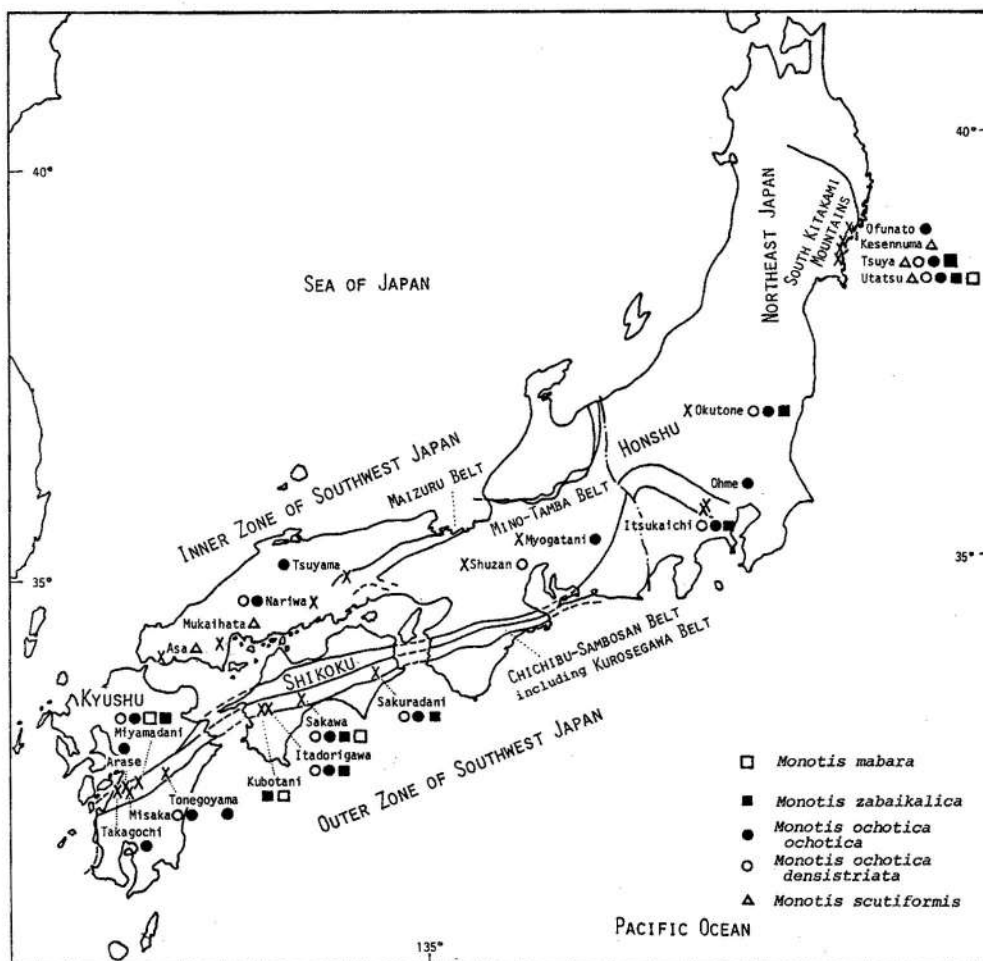
Figure 1. Map showing the distribution of Monotis species and the Monotis-bearing Upper Triassic formations in Japan.

2 TAXONOMIC PROBLEMS AND INTRASPECIFIC VARIATION

The classification of Monotis, both infra-specific and supraspecific, is now considerably confused owing to excessive splitting and typological treatment of specimens. More than 60 specific and infraspecific taxa have been proposed by various authors, as reviewed by Westermann (1973b) and Grant-Mackie (1978a). Keyserling (1848) described Monotis species as "Avicula ochotica minor", "A. ochotica media" and "A. ochotica major" from the coast of Okhotski Sea in northeast Siberia, all of which are trinominal and invalid now. Teller (1886) described the three forms from Verkhoyansk in northeast Siberia as "Pseudomonotis"

ochotica, disregarding Keyserling's second specific names, and proposed five additional varieties, namely "densistriata", "sparsicostata", "eurhachis", "ambigua" and "pachypleura". After then, many paleontologists have proposed and described several infraspecific taxa within this nominal species, and have added other closely related species. In Japan, for instance, Kobayashi (1935), Sakaguchi (1939), Kobayashi & Ichikawa (1949), Ichikawa (1951), Bando (1961), Nakazawa (1963, 1964) and Tamura (1965) described many species, subspecies and varieties, most of which were critically listed by Hayami (1975, p.68-71). Several "subspecies" of a single species or some closely related "species" were often reported from one and the same local-
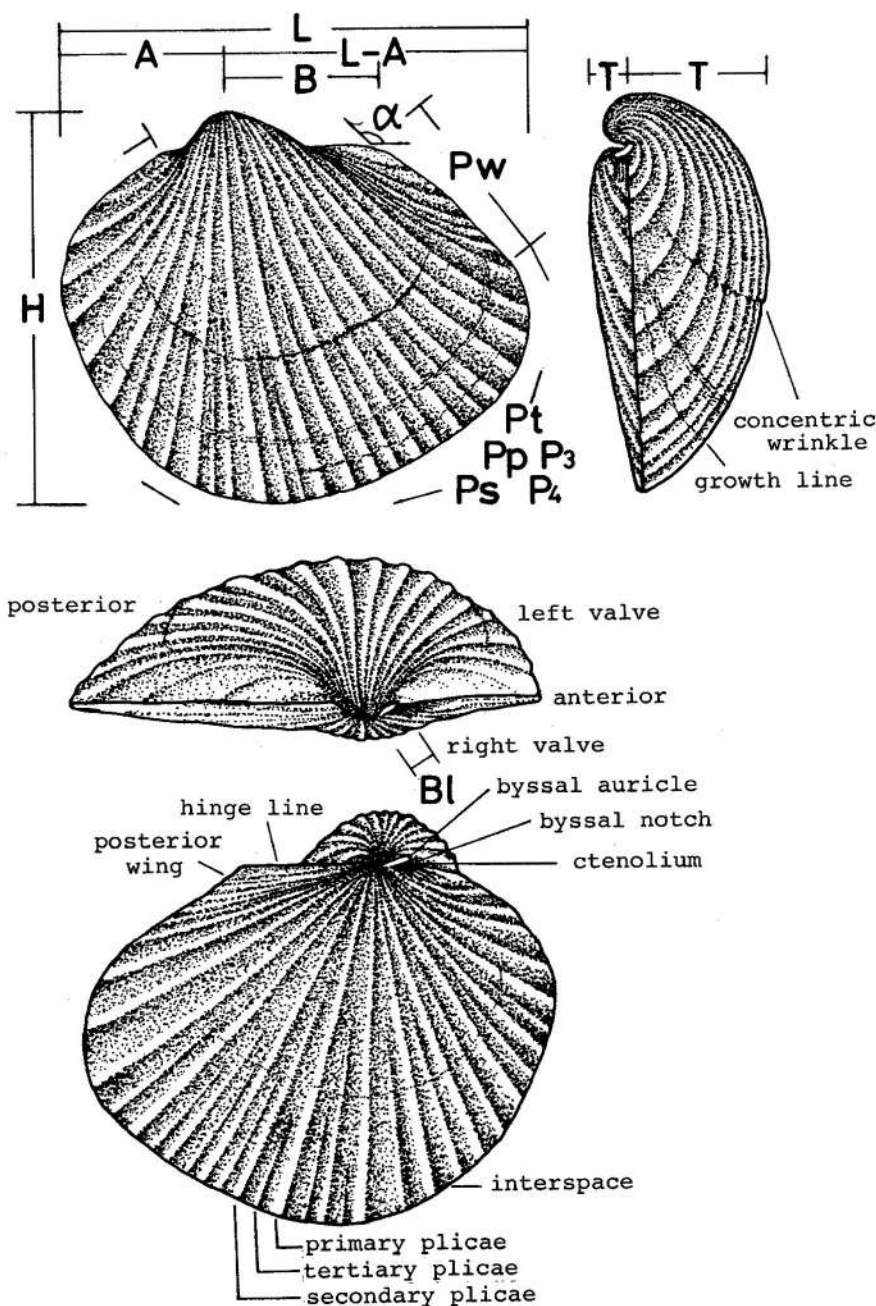
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Figure 2. Reconstruction of Monotis ochotica ochotica (Keyserling) showing some important morphological features and definitions of statistical parameters of Monotis valves. L: length; H: height; T: thickness; A: preumbonal length; L-A: posterior length; B: length of posterior auricle; a: truncation angle of posterior wing; Pt: number of total radial plicae; Pp: number of primary plicae; Ps: number of secondary plicae; P3: number of tertiary plicae; P4: number of fourth-order plicae; Pw: number of radial plicae on posterior wing; B1: length of byssal auricle.

Table 1. Correlation chart of Monotis zonations in the Utatsu area.

	This paper	Nakazawa, 1964		Onuki and Bando 1958		Ichikawa, 1954		Shimizu and Mabuti, 1932
Norian	Monotis zabaikalica / Monotis mabara	E	zabaikalica	C4	zabaikalica semiradiata	S7	zabaikalica	Pseudomonotis sp.nov.
	Monotis ochotica ochotica		Eb pachypleura / Ea ochotica (ochotica)	C3	ambigua pachypleura / ochotica var. eurhachis / ochotica	S6	ochotica eurhachis pachypleura / S5 ochotica eurhachis ochotica / ambigua ochotica densistriata	ochotica / ochotica var. pachypleura
	Monotis ochotica densistriata	D	ochotica densistriata	C2	ochotica var. densistriata / multistriata	S4	ochotica densistriata	ochotica var. densistriata
	Monotis scutiformis	C	typica (Cb aff. iwaiensis / Ca typica)	C1	scutiformis / scutiformis var.typica / scutiformis var.kolyma / scutiformis var. tenuicostata	S3	typica ochotica densistriata	ochotica var. densistriata / Placites aff. oxyphyllusites / Arcestes aff. oligosarcus / Dictyoconites sp.nov.
		B	Dictyoconites nipponicus			S2	Dictyoconites	
Carnian		A	Tosapecten cf. suzukii			S1	Tosapecten / Oxytoma	

Saragaizaka Formation · Hiramatsu Formation · Chomomori Formation · Shindate F. · Upper Formation · Middle Formation · Lower Formation

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ity. Considering the modern concept of systematics, such coexistence of many subspecies or closely related species seems to be rather unlikely.

Hayami (1969, p.378) criticized the hitherto proposed typological classification of Monotis species from Japan, and preferred a hypothesis that all the specimens of Monotis in a fossil bed belong to one and the same species. His monospecific hypothesis of Monotis faunas is here taken as an important premise, and I have attempted to test it by means of biometrical and other methods, taking intrapopulational variation into account. During the present study wide morphological variation has been often recognized within one and the same fossil population.

Excellent discussions about the systematic position of Monotis have been provided by Ichikawa (1958), Westermann (1962, 1973a, b) and Grant-Mackie (1978a). Though there are few problems about its generic validity, different opinions have been expressed about infrageneric division. When Ichikawa (1958) settled the previous taxonomic confusion, he divided the genus into two subgenera, namely Monotis (s. s.) Bronn, 1830 and M. (Entomonotis) Marwick, 1935. Westermann (1966) did not accept this dichotomy, but subsequently (1973b) classified Monotis into five species groups on the basis of morphologic similarity and geographic distribution; namely the M. salinaria, M. ochotica, M. subcircularis, M. scutiformis and M. zabaikalica Groups. Then he assumed their dispersal history during Norian time. A detailed historical review till 1977 was given by Grant-Mackie (1978a). In the same paper he proposed the division of Monotis into five subgenera, emending Westermann's grouping and proposing the latter three subgenera; i.e. Monotis (s. s.), M. (Entomonotis), M. (Eomonotis), M. (Inflatomonotis) and M. (Maorimonotis). The distribution of the last two subgenera is restricted to the Maorian province.

Recently, Tozer (1980), though provisionally, proposed tripartite generic division, namely with Monotis Bronn (including Entomonotis Marwick), Eomonotis Grant-Mackie and Maorimonotis Grant-Mackie as distinct genera.

Grant-Mackie's subdivision was based on the shell outline, degree of inequivalveness, shell ornamentation, and the separation and plication of the posterior wing. In some cases variable states of these characters, on which his subgeneric division was based, are found even in a single population sample. So far as I have observed Japanese samples, such an unstable

character is rather inadequate as a diagnostic criterion for subgeneric separation. For the time being, I follow Westermann's classification with some emendation, and do not use any subgeneric division.

Considering the problems examined above, Japanese Monotis samples should be biometrically investigated, because of its gregarious and successional stratigraphic occurrence (Fig.2). The great variability of the outline and ornamentation in each Monotis sample may be partly due to a secondary deformation, but is mainly attributable to wide original intrapopulational variation. As long as I use several parameters such as L/H, L-A/A, L-A/B and Pp, most of the samples do not show any significant bimodal or polymodal distribution (which suggest the coexistence of two or more species) though the distribution of Pp of M. zabaikalica indicates an exception, as described later. Other qualitative characters also indicate the same tendency. It is concluded that Japanese Monotis species can be classified into four species and one subspecies, namely Monotis scutiformis (Teller), M. ochotica densistriata (Teller), M. ochotica ochotica (Keyserling), M. zabaikalica (Kiparisova) and M. mabara (Kobayashi & Ichikawa).

3 STRATIGRAPHIC DISTRIBUTION OF MONOTIS SPECIES IN JAPAN (Table 1)

Stratigraphically documented serial samples of Monotis, which are indispensable for evolutionary studies, have been looked for throughout Japan. Though such samples were obtained only in a few areas, all the incomplete Monotis sequences can be compared with the standard Shirayamazawa section in the Utatsu area. The absence of any good key bed and index fossils such as ammonites and conodonts, makes accurate correlation difficult. The Monotis-bearing part does not exceed 150 meters in thickness in any area. The monotis succession confirmed in the Utstsu area seems to be compatible to other areas in Japan. The present quadripartite division may be similar to Onuki and Bando's (1958) and Nakazawa's (1964). The constituent species that comprised each zone were characterized by co-existence of one dominant species and a few subordinate species (or subspecies).

4 EVOLUTIONARY CHANGES OF MONOTIS FROM JAPAN

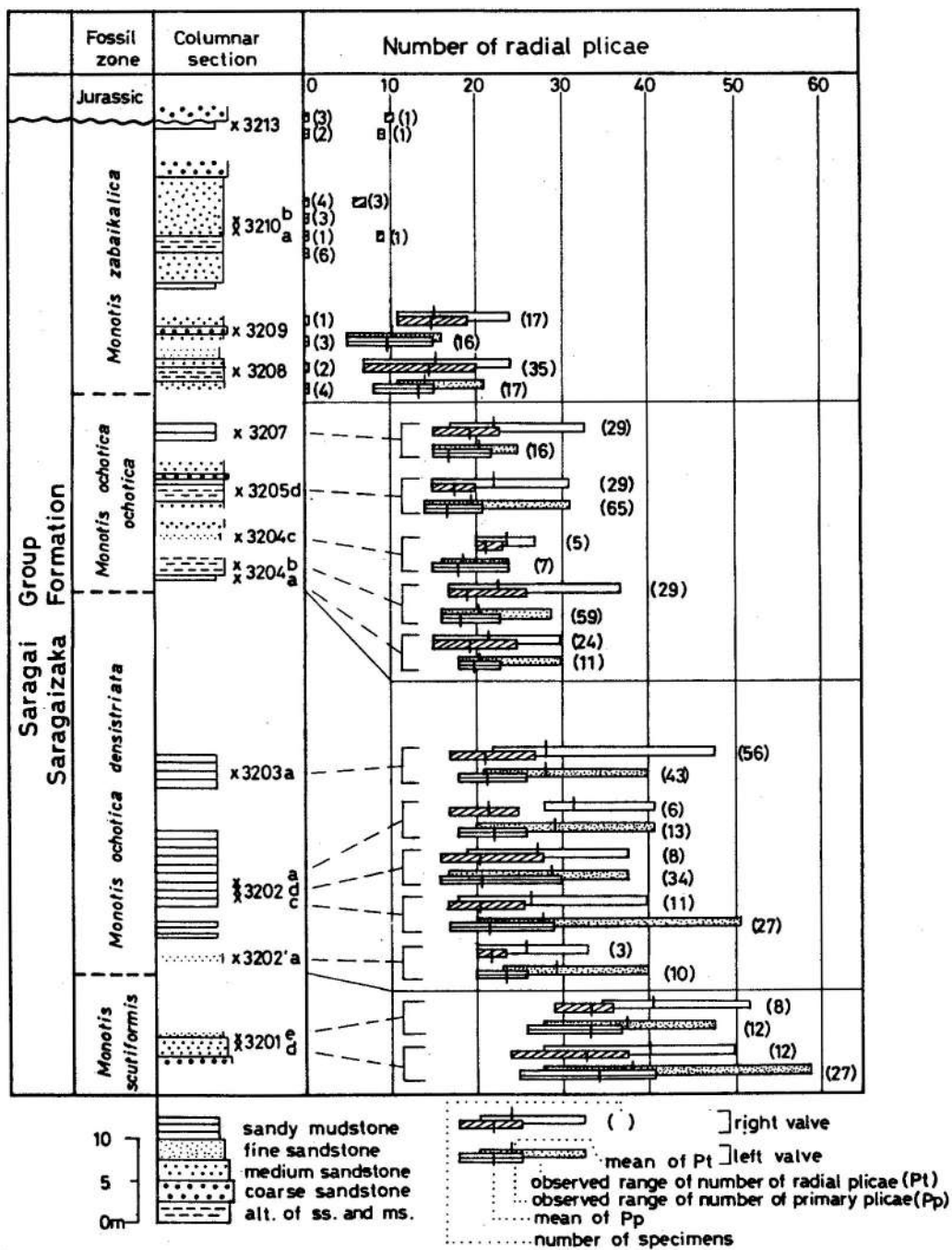Generally speaking, evolutionary changes in a widely distributed taxonomic group

Figure 3. Chronological changes of number of radial plicae in sequential samples from the Shirayamazawa section of the Utatsu area.
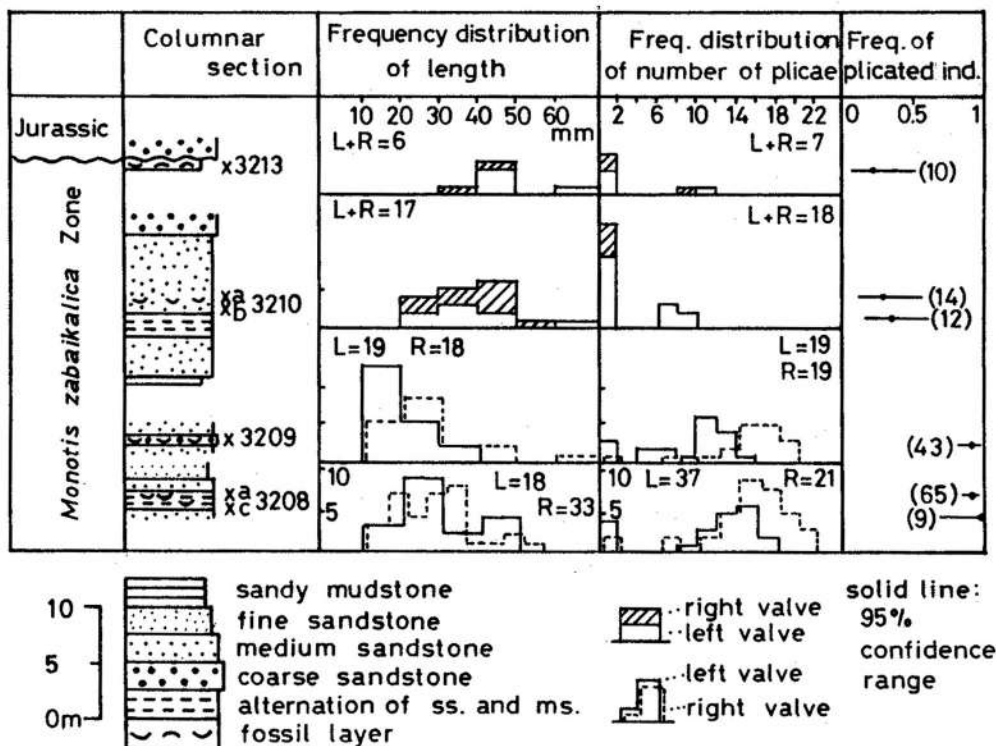
Figure 4. Chronological changes of number of radial plicae and frequency of plicated valves in Monotis zabaikalica(Kiparisova) from the Shirayamazawa section of the Utatsu area.

should not be discussed only on the evidence from local areas. In this case, however, several Monotis sequences in Japan, show essentially the same stratigraphic changes in various morphological characters. Although precise correlation among these sequences is now difficult, I believe that the observed morphological shift is mostly evolutionary instead of ecophenotypic.

4.1 Chronological changes in two selected sequences

1. Monotis sequence in the Utatsu area
The observed ranges and means of Pt and Pp in each sample are shown together with the stratigraphical columnar section at Shirayamazawa (Fig.3). The values of Pt and Pp seem to change abruptly at some horizons between 3201e and 3202'a, and between 3207 and 3208. But the change is not so clear at the boundary between the M. ochotica densistriata and M. ochotica ochotica Zones. In the two species, M. ochotica and

M. zabaikalica, Pp tends to decrease in upward sequence. In other parameters, however, it is difficult to detect any significant changes with certainty. Gradual changes can be recognized within the M. ochotica Zone, namely the mean of Pp gradually changes from 23.1 in sample 3202'a (left plus right valves) to 16.7 and 17.6 respectively in left and right valves of sample 3205d. Sample 3207 has a wider variation in strength of plicae, especially on the posterior wing.

On the other hand, M. zabaikalica shows a different mode of chronoligcal change (Fig.4): Pt and Pp decrease generally with increasing frequency of non-plicated valves. Furthermore, weakening of radial sculpture is also observed throughout the ontogeny of M. zabaikalica. In many specimens radial plicae decrease and become obscure with growth. They often disappear simultaneously at a certain concentric wrinkle. In upward sequence, the stage at which radials disappear becomes accelerated. Concentric wrinkles of folds commonly appear instead of radial sculpture, prob-
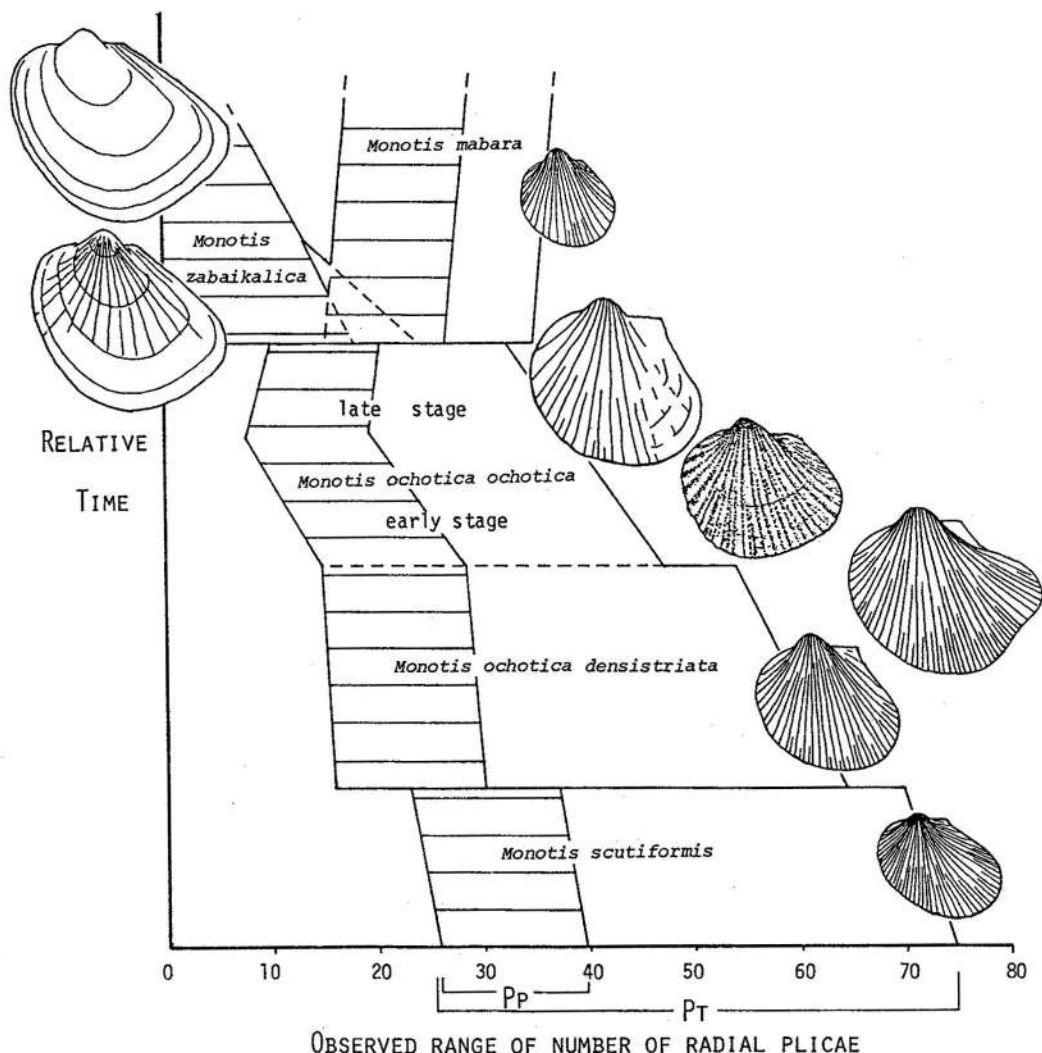
Figure 5. Inferred phylognetic trend of Japanese Monotis.

ably for the sake of maintaining shell strength. The stage of the first appearance of concentric wrinkles is also accelerated.

2. Monotis sequence in the Miyamadani area
In the Miyamadani area, M. ochotica densistriata, M. ochotica ochotica and M. mabara in upward sequence show interesting morphological changes. The frequency distribution of Pp does not seem to show any significant chronological change. But the earlier samples belonging to M. ochotica densistriata are characterized by more numerous higher-ordered plicae. M. ochotica ochotica of late stage, which contains abundant "sparsicostata" (Teller's (1886) variety) type individuals, appears after a barren part. Toward the upper horizon the frequency of "sparsicostata" type individuals decreases, while that of the "eurhachis" type individuals increases. M. ochotica ochotica is represented by the later samples, which are composed of individuals with slightly larger numbers of Pp and smaller numbers of higher-order plicae. The latest species, M. mabara, represented by the latest samples, may indicate that Pp increases with time, though the sample size is small.

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4.2 Inferred evolutionary changes of Monotis

The inferred evolutionary changes of Monotis from Japan can be schematically shown in Fig.5, where the perpendicular axis represents relative time (thickness of strata) and the horizontal axis shows observed ranges of Pp and Pt.

M. scutiformis is the first species in the Monotis sequence. It has rather obliquely elongate outline with numerous fine radial plicae, and the later samples probably show slight decrease in Pp and Pt.

The second species, M. ochotica shows not only fairly wide intrapopulational variation but also rapid chronological change. The early populations of this species are recognized as a chronological subspecies, M. ochotica densistriata. Because the small specimens of this subspecies, particularly from the lower horizons, are similar to those of M. scutiformis, it is inferred that M. ochotica was probably derived from M. scutiforms. Within M. ochotica densistriata, Pp decreases gradually and slightly with time. M. ochotica ochotica has fewer, stronger and wider plications than the preceding subspecies. It shows at first rather narrow intrapopulational variation in ornamentation, but the variation later becomes extremely wide. Some individuals have obscurely plicated but irregularly wrinkled posterior zones, like M. zabaikalica, and other individuals show fine plication similar to M. mabara. But in the latest stage there is a trend characterized by increase of Pp, in spite of the decrease of higher-order plicae. Among samples from different areas, considerable difference of Pp can be recognized. At present, it is, however, difficult to determine whether this difference is due to geographic variation or chronological change.

M. zabaikalica and M. mabara coexist in the same fossil beds in the Utatsu, Sakawa, Kubodani and Miyamadani areas, though their relative frequency varies among these areas. While the stratigraphic ranges of the two species partly overlap, those of M. mabara and M. ochotica ochotica do not seem to overlap each other. In the serial samples of M. zabaikalica radial sculpture becomes much weaker and concentric wrinkles more prominent with time. The morphological similarity between the young shell of M. zabaikalica and M. ochotica ochotica as well as their stratigraphic relation suggests that the former was derived from the latter.

On the other hand, M. mabara is also similar to the densely plicated representatives of M. ochotica ochotica. M. ochotica may be ancestral to M. mabara.

Let us consider the phylogenetic pattern of Monotis in Japan and east Siberia. The chronological change of shell morphology from M. scutiformis to M. ochotica ochotica via M. ochotica densistriata is attributable to phyletic evolution without any speciation, although this represents only one of the lineages of Monotis at that time. But in the last stage of the evolution, the increase of intrapopulational variation might have been followed by the divergence into two lineages, represented by M. zabaikalica and M. mabara. Although the morphology of these two species is predicted by some specimens in the samples of M. ochotica ochotica, this does not necessarily mean sympatric speciation. In accordance with widely accepted evolutionary theory, reproductive isolation between the two lineages seems to have been completed by some allopatric speciation before the first appearance of M. mabara.

In the lineage from M. scutiformis to M. ochotica ochotica, the morphological change is regarded as paedomorphic or neotenic, because the morphology of immature growth stages of the ancestral species, especially in shell outline and radial plication, was followed by the mature stage of the descendant species. On the other hand, the phyletic change of ornamentation in M. zabaikalica may be regarded as peramorphic or accelerative, because the disappearance of radial plicae became much accelerated.

Ichikawa (1954) already recognized the following trends of morphological characters, mainly on the basis of materials from the Utatsu area:

1. The number of orders of radial plicae increased from 1 to 3 at first, then decreased from 3 to 1, and finally radial plicae disappeared. The number of radial plicae decreased directionally.

2. Ligament area became higher.

3. Shell size increased with time.

Westermann (1973a, b) suggested probable phylogeny of Monotis on the basis of such morphological features as convexity and posterior auricles, and proposed a scheme of geographic dispersal in which the species with weakly plicated and obscurely delimited posterior wing were followed by more variably plicated or rather smooth and wrinkled species with well developed smooth wing. In other words, the M. scutiformis (= his M. typica) Group was said to have diversified into three species groups, namely North and Southwest Pacific M. och-
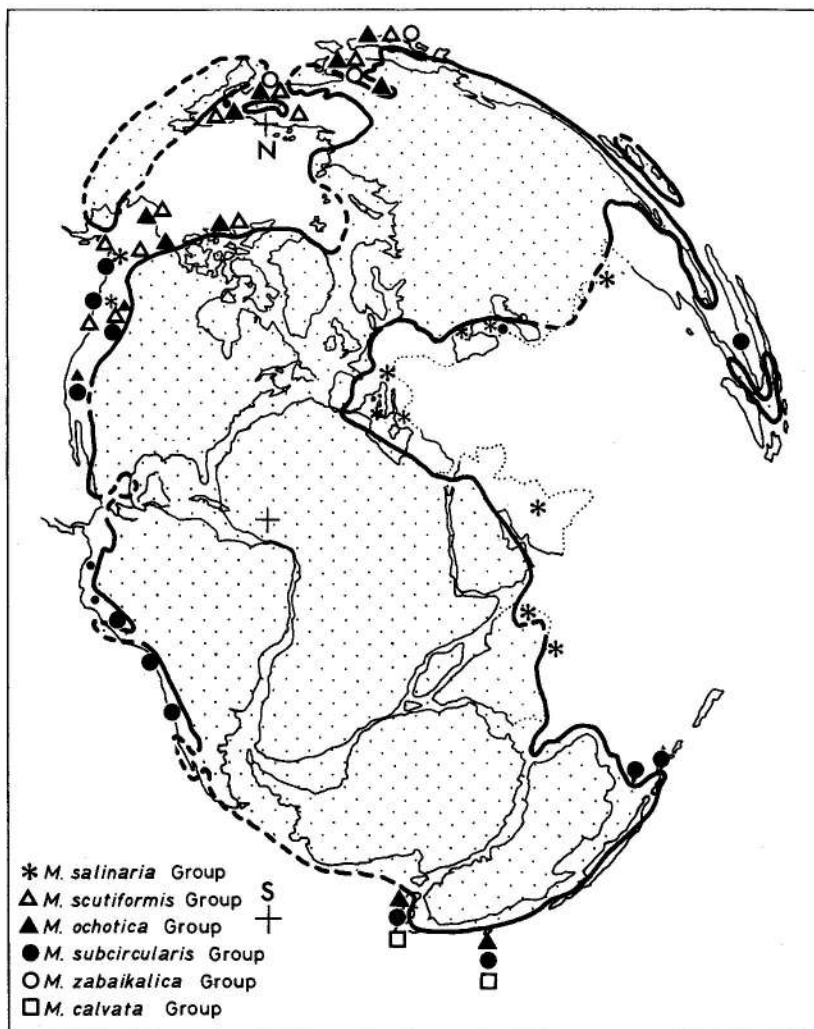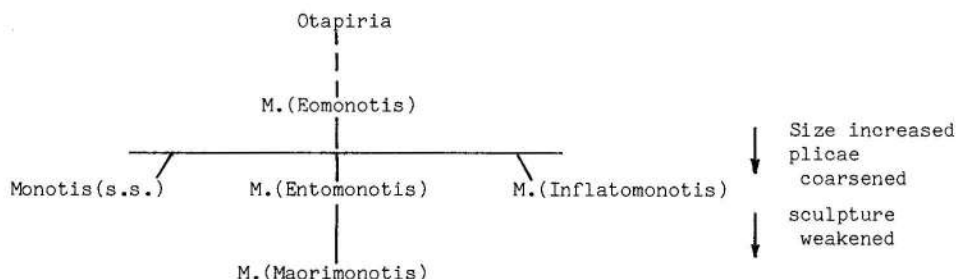
Figure 6. World-wide distribution of Monotis. Species groups and their distributions are adapted from Westermann (1973b) and others. Palaeo-continental reconstruction in Norian age is mainly adapted from Smith & Briden (1977) and Damborenea & Mancenido (1970). Dotted area: land; broken line: presumed shoreline; N and S: inferred pole positions.

otica, Southwest and East Pacific M. sub-circularis and Tethyan M. salinaria Groups (Fig.6).

Recently, Grant-Mackie (1980a) commented on the evolution of Monotis: "Evolution would have preceded from a small light subequivalved, possibly epi- or pseudo-planktonic ancestor (e.g. Otapiria) to produce firstly Eomonotis, then by size increase and ribs coarsening to Monotis s.s and Entomonotis, followed by weakening of sculpture and reduction of ears (Maori-monotis)". The idea is represented as follows:

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                        Otapiria
                           |
                           |
                    M.(Eomonotis)
                           |                                      Size increased
  _____/_____|_____                  plicae
 /                         |                       \                 coarsened
Monotis(s.s.)       M.(Entomonotis)       M.(Inflatomonotis)    ↓
                           |                                      sculpture
                           |                                     weakened
                    M.(Maorimonotis)                            ↓
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Otapiria, which is said to have appeared in
Carnian time, before the first appearance
of Monotis, is the most closely allied
genus. But there is no reliable evidence
of the ancestor-descendant relation bet-
ween the two. Though Maorian Eomonotis
does not seem to be the same as the M.
scutiformis Group, the first species in
the Maorian province is also finely plic-
ated. According to Grant-Mackie, the sub-
genus might have diversified into three
subgenera. Inflatomonotis and Maorimonotis
proposed by him are restricted to the
Maorian province. The latter, assigned to
the M. calvata Group in this study, is an
aberrant, non- or weakly-plicated form
similar to M. zabaikalica.

Compared with the previous three authors'
ideas, the coarsening of plicae and weak-
ening of sculpture are also recognized in
the Japanese lineage from M. scutiformis
to M. zabaikalica. Generally Westermann's
(1973b) idea can be accepted, although M.
subcircularis and M. salinaria Groups dis-
cussed by him do not occur in Japan. As
regards Grant-Mackie's scheme, I think that
the phylogeny of Monotis should not necess-
arily be interpreted at subgeneric level
but at species level, because the important
unit for evolution is an evolutionary spe-
cies. The phylogenetic pattern of Japanese
Monotis, however, is partly similar to his
scheme. Almost all the species of his
Maorian Eomonotis, Entomonotis and Inflato-
monotis can be included in the M. ochotica
Group. As in the Japanese lineage, the
middle evolutionary stage seems to be
characterized by wide intraspecific mor-
phological variation. The last stage may
be represented by the coexistence of the
M. calvata and M. ochotica Groups.

5 PALEOBIOGEOGRAPHY OF MONOTIS

5.1 Paleobiogeography of Monotis in Japan
    and east Siberia

The Monotis fauna everywhere in Japan is

usually monospecific, but the constituent
species change from horizon to horizon.
It does not show any conspicuous provinci-
ality. M. scutiformis has not yet been
found from the Outer Zone of Southwest
Japan,and M. mabara does not occur in the
Inner Zone.This may be due, however, to the
incompleteness of these Monotis sequences.

All the Japanese species and subspecies
of Monotis except M. mabara are taxonomi-
cally identical with those from east Sib-
eria (especially Verkhoyansk and Kolyma
Mountains; Kiparisova et al., 1966).
Although the last species, M. mabara, seems
to be endemic to Japan, it was probably a
daughter species from the main stock which
was commonly distributed both in east
Siberia and Japan. Whatever horizontal
movement of suspect terranes took place,
the main part of the Japanese Islands must
have been biogeographically connected with
east Siberia in Late Triassic times. The
faunal connection is also well documented
by a number of other Carnian-Norian bi-
valves called Kochigatani Fauna in Japan,
which occur commonly between the two re-
gions.

In Japan, Monotis occurs in sediments of
various grain size from coarse-grained sand-
stone to sandy mudstone, in addition to
sandy limestone and tuff. The lithology
indicates relatively shallow shelf environ-
ments. On the other hand, in the Tethyan
region, the micritic limestone called the
Hallstatt facies is characterized by the
occurrence of Monotis salinaria and is
believed to represent a bathyal or pelagic
environment.

In the Sambosan Belt of the Outer Zone
of Southwest Japan, however, the Carnian
to Norian faunas are quite different from
those of other northern regions including
Monotis-bearing formations, as pointed out
by Tamura (1972, 1981, 1983). They contain
obvious Tethyan elements such as Gruene-
waldia, Costatoria and Gervillia (Cultrio-
psis) which show close affinity with
species from the St. Cassian Formation in
the Alps, though Monotis does not occur
there. Recently, Tamura (1981, 1983) dis-

covered megalodontid-bearing limestones
with Triadomegalodon sp. cf. tofanae
(Hoernes) and Dicerocardium kuwagataforme
Tamura of Norian or Rhaetian age in east-
ern Kyushu. He inferred some tropical la-
goonal environment of a volcanic island as
the depositional site. Some part of the
limestone is somewhat similar to the Hall-
statt Limestone, but Monotis has not yet
been found. The megalodontid and other
bivalve faunas of the Sambosan Belt as
well as its sedimentary facies show strong
contrast with the Monotis and other Carn-
ian-Norian Kochigatani faunas in the nor-
thern adjacent terranes of Southwest Japan.
There is a possibility that the Sambosan
Belt may be a suspect terrane of southern
origin, which had accreted to the northern
mainland of Japan.

5.2 Paleobiogeography of Monotis in the
world

The worldwide geographical distribution of
Monotis is summarized in Fig.6, assigning
various proposed species into six species
groups in agreement with Westermann (1973b)
and Grant-Mackie (1978a). The M. ochotica,
M. subcircularis and M. salinaria Groups
are the same as Westermann's, but his M.
typica Group is here called the M. scuti-
formis Group. M. calvata and M. routhieri
from the southern hemisphere were included
in the M. zabaikalica Group by Westermann
(1973b), but they are here separated as
the M. calvata Group (Grant-Mackie 1976).
They were regarded by Grant-Mackie (1978d)
as constituting the new subgenus Maorimon-
otis together with two other species.

As pointed out by Westermann (1973b) and
Tozer (1980), several major Monotis prov-
inces can be recognized; for example, the
Western to Northeastern Pacific province
is characterized by the M. ochotica Group,
the Eastern Pacific province by M. subcir-
cularis, the Tethyan province by M. salin-
aria, the Northwestern to Northeastern
Pacific province by M. scutiformis, the
Northwestern Pacific province by M. zab-
aikalica, and the Southwestern Pacific
province by M. calvata.

Recently, Tozer (1982) discussed the
distribution of Triassic marine inverte-
brate faunas in North America considering
plate and terrane movements. Current dev-
elopment of plate tectonic theory has
presented an interpretation in which the
greater part of the North American Cordil-
leran margin is actually a mosaic of
terranes which "seem to have been swept
from far reaches of Pacific Ocean before
collision and accretion into the Cordil-

leran margin mostly in Mesozoic to early
Cenozoic time (Coney et al. 1980, p.329)"
(Tozer 1982, p.1080). He adopted the term
"suspect" for the exotic terranes whose
origin is uncertain, and the term "plate-
bound" for the terranes that were deposited
on a continental plate in situ. The North
American Cordilleran faunas were classified
into three types, namely the low, mid and
high paleolatitude faunas (LPL, MPL, HPL)
regardless of plate-bound or suspect.
Monotis occurs both in plate-bound sequen-
ces and in suspect terranes. Tozer thought
that M. salinaria in the Hallstatt Lime-
stone facies was an indicator of LPL, M.
subcircularis of MPL or LPL and Eomonotis
(M. scutiformis Group in this paper) and
M. ochotica of HPL or MPL, considering the
faunal composition, sedimentary facies and
geographical distribution of faunas in
Westermann's scheme.

During the preparation of Fig.6, the need
arose to explain various disjunct distri-
bution of Monotis species; for example, M.
subcircularis in Borneo (Tamura & Hon 1977),
M. salinaria in Mexico and east Siberia,
etc. These distributions could be explained
if the collision and accretion of suspect
terranes were accepted, but this is possi-
bly an untestable hypothesis.

Recently, Grant-Mackie (1978a-c, 1980b,
c) described a number of Monotis species
from New Zealand. Though detailed compari-
sons still remain to be done, I presume
that some species of Eomonotis and Entomon-
otis proposed by him are synonymous with,
or closely related to, the east Asian
species. Because the Maorian monotids were
too finely split, the true diversity may
not be so high. Wider assessment of the
intraspecific variation appears to be nee-
ded. Other Maorina bivalve faunas of Carn-
ian to Rhaetian age indicate considerable
differences from the Northeastern Pacific
and Tethyan regions, as was summarized by
Kobayashi & Tamura (1983a, b).

6 CONCLUSION

Monotis seems to be an interesting fossil
organism because of its worldwide geogra-
phic distribution, gregarious and exclusive
occurrence, and rapid morphological shifts
with time. The classification, stratigraphic
distribution and evolutionary changes are
examined here on the basis of Japanese
materials, but this is only the first step
in a comprehensive study of Monotis,
because the evolution of a taxonomic group
should be generally clarified on the basis
of various evidence in the world. In this
study, any mechanism which caused evolu-

tionary change described before, can hardly be recognized due to incompleteness of the fossil record. The evolutionary changes of Japanese Monotis, however, provide data on phyletic evolution almost along a single lineage. When considered within M. ochotica and M. zabaikalica, it does not appear to support stasis maintained in punctuated equibrium theory. Anyway, because this evolutionary transition possibly occurred during only a few million years, the evolutionary rate of Monotis must be extremely high.

The geographic distribution and provinciality of Monotis are undoubtedly important for Late Triassic paleobiogeography. Four major biogeographic regions can be recognized; they are, East Asia (east Siberia and Japan) characterized by the M. scutiformis and M. zabaikalica Groups, Tethys (Alps, Himalayas, etc.) by the M. salinaria Group, western rim of the Americas (Alaska, British Columbia, Nevada, Peru and Chile) by the M. subcircularis Group and Maorian (New Zealand and New Caledonia) by the M. calvata Group. Each region is characterized by one or a few species groups of Monotis, but the phylogenetic relation among the groups and ecology must be further explored by more extensive comparative studies.

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(J): in Japanese; (J+E): in Japanese with English abstract; (R): in Russian

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Shallow Tethys 2

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Shallow Tethys 2 — *Proceedings of the international symposium on Shallow Tethys 2, Wagga Wagga, 15-17 September 1986*
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There is a new wave in geoscience. It has been gathering and gaining momentum since 1960 and is posed to break in Tethys, the fabled ocean-goddes of Greek legends adopted by geologists and geographers since Suess and Wegener to signify an ancient ocean, dividing northern Laurasia and southern Gondwana from the Palaeozoic until the Neogene. New results of field mapping and new data from fossil collections are reviewed and reported in *Shallow Tethys 2*. The resulting geotectonic and biogeographic reassessments fundamentally alter existing ideas. No longer can Tethys be conceived as simple, vast, wedge-shaped and deep. Rather it was complex, comprising shallow epicontinental basins interconnected by relatively narrow deeper sealanes and intervening large and smaller continental blocks – until the new dawn of the Cenozoic and the generation of familiar modern oceans.

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