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The Conodonts *Hindeodus*, *Isarcicella* and *Sweetohindeodus* in the Uppermost Permian and Lowermost Triassic

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Key words: Conodonts, *Hindeodus, Isarcicella, Sweet*ohindeodus, P/T boundary.

Abstract

Hindeodus REXROAD & FURNISH, 1964 and Isarcicella KOZUR, 1975 belong to the stratigraphically most important fossils near the Permian-Triassic boundary. The first appearance of *H. parvus* (KOZUR & PJATAKOVA) in the phylomorphogenetic lineage *H. typicalis - H. latidentatus praeparvus - H. parvus* is the best marker for the P/T boundary. Some representatives of *Hindeodus* and *Isarcicella* are insufficiently known. Consequently, all known *Hindeodus* and *Isarcicella* species from near the P/T boundary, are redescribed or discussed. *Hindeodus parvus erectus* n.subsp., *H. julfensis wardlawi* n.subsp., *H. latidentatus praeparvus* n.gen. with two species, *Sweetohindeodus bidentatus* n.gen. n.sp. and *S. tridentatus* are proposed.

1. INTRODUCTION

Strong provincialism during the Permian makes the correlation of the Boreal and Notal faunas with those of the tropical Tethyan realm difficult. This provincialism continued through the uppermost Permian Changxingian Stage and the very base of the Triassic (*H. parvus* Zone), where the tropical faunas of the central Tethys and the Boreal and Notal *Otoceras* faunas are very different.

Almost all fossil groups are strongly influenced by the Permian provincialism. The ammonoids are very different and fusulinids are even unknown in the Boreal realm above the Roadian. Also Tethyan brachiopods are rather different from Boreal and Notal representatives that show often a bipolar distribution.

Conodonts are only slightly affected by the Permian provincialism. For instance, *Vjalovognathus* KOZUR is restricted to the temperate and cool water of the margin of eastern Gondwana and the peri-Gondwana Tethys. Ribbed species of *Mesogondolella* KOZUR are restricted to shallow pelagic warm water deposits, and are therefore missing in the cold palaeopsychrospheric environments (KOZUR, 1991a, b) of the Permian oceans and deep water deposits of open sea margins. *Clarkina* KOZUR also shows distinct provincialism. *C*. rosenkrantzi (BENDER & STOPPEL) is restricted to either temperate or cool water areas of the Arctic and the peri-Gondwana Tethyan margin. Other species, such as *C. changxingensis* (WANG & WANG), occur both in the Arctic (e.g. in the lower *O. boreale* Zone of Setorym River in NE Siberia) and in the tropical Tethys (from Sicily to South China). Other *Clarkina* species (see section 3) prefer the tropical realm or are restricted to this area. With the establishment of a mondially rather uniform fauna a little above the base of the Triassic, advanced representatives of the *C. carinata* group are also present globally since the *I. isarcica* Zone.

Hindeodus REXROAD & FURNISH shows no provincialism, occurs across the P/T boundary and underwent rapid morphological changes within the Changxingian and lowermost Triassic. This genus is therefore best suited for defining the P/T boundary within a phylomorphogenetic lineage. The development from H. latidentatus praeparvus n.subsp. to H. parvus KOZUR & PJATAKOVA can be observed in continuous sections with temperate to cool water faunas of the Boreal realm (Greenland) and at the peri-Gondwana margin of the Tethys (Kashmir, Salt Range), as well as in continuous sections in the tropical realm (e.g. Southern Alps, Hungary, Sicily, Central Iran, Transcaucasia, South China). The first appearance of H. parvus within this phylomorphogenetic lineage is therefore of extraordinary importance for definition of the P/T boundary. This event occurs, for instance, in the middle part of Boundary Bed 2 at Meishan (South China), so far regarded by the present author as the most suitable candidate of the global stratotype section and point (GSSP) for the base of the Triassic (Figs. 1, 2). However, in a country, like China, an official state guaranted permanent access to Meishan for all scientists is necessary, before Meishan can be regarded as an official candidate for this GSSP. This includes also free sample transport out of China without custom barriers and special expensive allowness in the frame of cooperation of Chinese scientists with foreign institutions because free access means not only the possibility and allowness for everybody to visit a GSSP in a kind of "geotourism", but also to study it.

In the present paper the taxonomic status of the Upper Permian and Lower Triassic *Hindeodus* and *Isarcicella* species is considered, because the separation of some species was not well known in the past. Three

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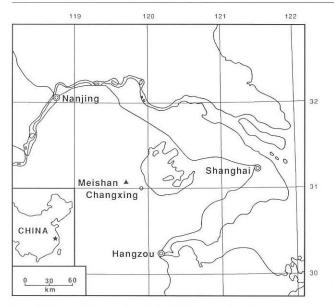


Fig. 1 Geographical setting of the Meishan section. Star represents location of the Meishan section in South China.

new *Hindeodus* species/subspecies and the new genus *Sweetohindeodus* with two new species are proposed. Moreover, the importance of the first appearance of *H. parvus* for the definition of the P/T boundary and related problems of the facies control for the distribution of *Hindeodus* and gondolellids near the P/T boundary are discussed.

2. THE IMPORTANCE OF THE FIRST APPEARANCE OF *Hindeodus parvus* FOR THE DEFINITION OF THE BASE OF THE TRIASSIC

H. parvus is easily determinable and readily separable from its forerunner *H. latidentatus praeparvus* (see systematic part), and its derivation is well documented by transitional forms. In several sections (as mentioned above) both taxa occur in a stratigraphic sequence connected by transitional forms.

H. parvus has a far wider distribution than any other conodont or ammonoid species near the P/T boundary, because it occurs both in ammonoid-free, shallow water, high energy Werfen facies and in pelagic facies with or without ammonoids. It is known so far from the Southern Alps, Dinarides, Hungary, Sicily, Crete, Transcaucasia (with the type locality), northwestern and Central Iran, Elburz, Kashmir, Salt Range, Himalaya, China, Japan, Greenland, Arctic Canada and western North America. This distribution covers the entire tropical Tethys, Circum-Pacific realm, cratonal North America, cold/cool water Boreal realm and the cool water to temperate peri-Gondwana margin of the Tethys. *H. parvus* therefore has no zoogeographic restriction. *H. parvus* is the first globally distributed species to appear after the minimum in faunal diversity indicated by the minimum in δ^{13} C. At Meishan, it appears 5 cm above that minimum.

The first appearance of H. parvus coincides with or slightly postdates the disappearance of upper Changxingian (uppermost Permian) gondolellids (TIAN, 1993, 1994; KOZUR, 1994a, b, 1995a, b), such as C. deflecta (WANG & WANG), C. dicerocarinata (WANG & WANG), C. postwangi (TIAN), C. sosioensis GULLO & KOZUR, C. subcarinata (SWEET) and Clarkina xiangxiensis (TIAN), and of Upper Permian Hindeodus, such as H. julfensis (SWEET) and H. latidentatus latidentatus (KOZUR, MOSTLER & RAHIMI-YAZD). It also coincides with the disappearance of Stepanovites KOZUR and slightly postdates the appearance of Ellisonia MÜLLER s.str., whereas C. changxingensis (WANG & WANG) and H. latidentatus praeparvus disappear in the lowermost part of the H. parvus Zone. Permian type ammonoids, such as Hypophiceras, Pleuronodoceras, Pseudogastrioceras and Pseudotirolites, and albaillellacean radiolarians disappeared immediately before the first appearance of H. parvus. Ophiceras appeared nearly contemporaneously with H. parvus. The globally distributed marine fungus Tympanicysta stoschiana (BALME) (Pl. V, Figs. 10, 11) disappeared close to the first appearance of H. parvus. The similarly widely distributed Isarcicella isarcica staeschei DAI & ZHANG and Claraia wangi (PATTE) appeared slightly above the first appearance of H. parvus. Thus, there are many biostratigraphic markers at or near to the base of the H. parvus Zone.

In all sections where the carbon isotope ratios have been investigated near the P/T boundary, the first appearance of *H. parvus* lies a little above the minimum in δ^{13} C. In sections where a lithostratigraphic event boundary is present, *H. parvus* appears a little above that boundary (e.g. in Meishan 15 cm above the eventstratigraphic boundary). Moreover, near the base of the *H. parvus* Zone a widespread anoxic event began. The P/T boundary defined with the first appearance of *H. parvus* is therefore also very close to a "natural boundary" sensu NEWELL (1994).

The first appearance of *H. parvus* is close to the traditional P/T boundary at the top of the Changxingian. In South China, this boundary was placed either somewhat above or below the first appearance of *H. parvus*. Until the monograph of ZHAO et al. (1978), it was placed at the base of the Claraia wangi Zone, which in the Meishan sections is 12 cm above the first appearance of H. parvus. KOZUR (1977a, 1989) defined the P/T boundary with the first appearance of *Isarcicella isarcica*, that is 8 cm above the first appearance of *H*. parvus. Subsequently, ZHAO et al. (1981) placed this boundary at the base of Boundary Bed 1 (= Base of the Transitional Beds) that is 15 cm below the first appearance of H. parvus. Still later, the lower part of Boundary Bed 1 ("White Clay") was again included in the Permian (because of its Permian conodont fauna) and

	Stage	Cone	odont Subzone	Formation	Lithostratigraphy and fauna	
		lsarcicella isarcica		Lower Qinglong or Yingkeng Formation	Bed 29 (26 cm) Gray, medium bedded, silty, dolomitic marls Ophiceratids; bivalve: Claraia wangi; brachiopod: Paryphella orbicularis conodonts: Clarkina carinata, Ellisonia transita, Isarcicella isarcica, I. ? turgida	
T R	Brahmanian ("Induan")				Bed 28 (4 cm) Grayish yellow illite-montmorillonite clay.	
н I					Conodonts: Hindeodus parvus, Isarcicella isarcica staeschei, I. ? turgida	
A S S I C		Hindeodus parvus			Bed 27 (16 cm) Light gray, silty limestone. Brachiopods: <i>Crurithyris flabelliformis, Fusichonetes pigmaea, Paracrurithyris pigmaea, Paryphella orbicularis, P. triquetra, Waagenites barusiensis;</i> The following detailed conodont distribution was found in bed 27:	
C					 12-16 cm: Clarkina carinata, C. changxingensis, Ellisonia transita, Hindeodus parvus, H. typicalis 8-12 cm: Clarkina carinata, C. changxingensis, Ellisonia transita, Hindeodus changxingensis, H. latidentatus, H. parvus (only primitive forms, transitional to H. latidentatus), H. typicalis, Isarcicella ? prisca 	
	I Changxingian	Clarkina deflecta Hindeodus latidentatus	Clarkina xiangxiensis		 4-8 cm: Clarkina carinata, C. deflecta, Hindeodus typicalis, Isarcicella ? prisca, Merrillina longidentata, Stepanovites sp. 0-4 cm: Clarkina carinata, C. changxingensis, C. procerocarinata, Ellisonia transita, Hindeodus changxingensis, H. latidentatus, H. typicalis, Isarcicella ? prisca 	
					Bed 26 (6 cm) "Black Clay" (dark-gray montmorillonite-illite clay, partly calcareous and silty).	
					Ammonoids: Hypophiceras changxingense, H. cf. martini, Otoceras ? sp., Metophiceras sp., Pseudogastrioceras sp.; bivalve: Peribositra baoqingensis; brachiopods: Araxathyris minuta, Cathaysia chonetoides, Crurithyris flabelliformis, Neochonetes convexa, Neowellerella pseudoutah, Paracrurithyris pigmaea, Paryphella orbicularis, P. sulcatifera, P. triquetra, Waagenites barusiensis, W. wongiana; conodonts: Clarkina cf. carinata, C. changxingensis, C. dicerocarinata, C. deflecta, C. meishanensis, C. cf. sosioensis, C. xiangxiensis, Hindeodus latidentatus	
P E					Bed 25 (4 cm) "White Clay" (light bluish gray, weathered yellowish white illite-montmorillonite clay).	
I					Conodonts: <i>Clarkina</i> cf. <i>carinata</i> , <i>C. changxingensis</i> , <i>C. deflecta</i> , <i>C.</i> cf. <i>meishanensis</i> , <i>C. xiangxiensis</i> , <i>Hindeodus latidentatus</i> ; non-fusulinid foraminifers: <i>Bradyina</i> sp., <i>Globivalvulina</i> sp., <i>Hemigordius</i> sp.	
A N				Upper Changxing Formation (Meishan Member)	Bed 24 e (20 cm) Dark gray bedded micrite.	
					Ammonoids: Rotodiscoceras sp.; brachiopods: Crurithyris flabelliformis, Neowellerella pseudoutah, Wellerella delicatula; conodonts: Clarkina cf. carinata, C. changxingensis, C. deflecta; fusulinids: Palaeofusulina sp.	
					Bed 24 d (23 cm) Dark gray, bedded wackestone with very thin bioclast- bearing calcareous mudstone interbeds.	
					Ammonoids: Pleuronodoceras mirificus, Pseudogastrioceras sp.; conodonts: Clarkina cf. carinata, C. changxingensis, C. deflecta, C. xiangxiensis, Hindeodus latidentatus; foraminifers: Palaeofusulina cf. sinensis, Geinitzina caucasica, Nodosaria netchajevi, Pachyphloia lanceolata	
			Clarkina postwangi		Beds 24 c and b (28 cm)Dark gray, bedded dolomitic packstone with thin clay interbeds.Conodonts: Clarkina changxingensis, C. deflecta, C. postwangi	
					Bed 24 a (10 cm) Dark gray, bedded wackestone, thin clay bed at the top. Conodonts: Clarkina cf. carinata, C. changxingensis	

Fig. 2 Lithology, faunal distribution and conodont zonation around the Permian-Triassic boundary in the Meishan section, South China. Beds 25 and 26 correspond to the lower Transitional Beds by YIN (1985) and to the Boundary Bed 1 by WANG (1994). Bed 27 corresponds to the upper Transitional Beds and to the Boundary Bed 2. Conodont distribution after KOZUR et al. (1996) and WANG et al. (1996).

the P/T boundary was placed at the base of the "Black Clay" (upper part of Boundary Bed 1), 11 cm below the first appearance of *H. parvus* (YIN et al., 1988; YANG et al., 1993). YIN (1993) and YIN et al. (1994) placed the P/T boundary at the base of Boundary Bed 2, which lies 8 cm below the first appearance of *H. parvus*, but defined the P/T boundary with the base of the *H. parvus*, but defined the P/T boundary with the base of the *H. parvus*, but defined the P/T boundary at a level 8, b) and WANG (1994, 1995a, b) placed the base of the Triassic at the base of the *H. parvus* Zone at a level 8 cm above the base of Boundary Bed 2 (middle part of Bed 27).

On the peri-Gondwana margin of the Tethys H. parvus appears within the O. latilobatum bed at Selong. O. latilobatum WANG & HE is a junior synonym of O. fissisellatum DIENER (KRYSTYN, in KRYSTYN & ORCHARD, 1996) and represents in the peri-Gondwana Otoceras faunas the Arctic uppermost O. boreale Zone or the level with the first very primitive H. parvus in Greenland, above the last O. boreale and below rich occurrences of Claraia stachei BITTNER of the lower Ophiceras commune Zone. The data presented by KRYSTYN (in KRYSTYN & ORCHARD, 1996) confirm the conodont correlations by KOZUR (1994b) that the peri-Gondwana O. woodwardi Zone is younger than the Arctic Otoceras faunas and represents the lower part of the Arctic O. commune Zone. As the Otoceras beds of the Selong section are strongly condensed, the first primitive H. parvus from the upper O. "latilobatum" bed may represent already the basal Otoceras woodwardi - Ophiceras bandoi Zone. The entire latter zone contains H. parvus nearly in all sections. Only in Kashmir, H. parvus appears within the O. woodwardi Zone, seemingly near to the first appearance of Ophiceras (MATSUDA, 1981). This may be explained either by insufficiant conodont data from the lowermost bed of the Otoceras fauna because the following bed contains already advanced specimens of H. parvus, or the Otoceras from the lowermost bed of the Otoceras fauna belongs to the O. boreale group (suture zone not yet re-studied according to the criteria elaborated by KRYSTYN in KRYSTYN & ORCHARD, 1996).

As the base of the Triassic was defined with the base of the *O. woodwardi* Zone in Central Himalaya, the base of the *H. parvus* Zone is very close to or coincides with the traditional base of the Triassic. It is, however, considerably younger than the base of the *O. concavum* Zone that is used to define the base of the Triassic in the Arctic.

YIN (1985, 1993), KOZUR (1994a, b, 1995a, b), PAULL & PAULL (1994), YIN et al. (1994), WANG (1994, 1995a, b), KOZUR et al. (1996), WANG et al. (1996), WIGNALL et al. (1996) and JIN et al. (1996) used the base of the *H. parvus* Zone as base of the Triassic. Following YANG et al. (1987), YIN et al. (1994) proposed section D at Meishan (South China), the stratotype of the Changxingian Stage, as GSSP of the P/T boundary. WANG (1994, 1995a, b) proposed the quarry Z (Zhongxin Dadui section) of the Meishan section as GSSP, following SHENG et al. (1984). WANG et al. (1996) left open the decision to use section D or the Zhongxin Dadui section, about 0.5 km east of section D as GSSP for the P/T boundary. KOZUR et al. (1996) regarded Meishan as a laterally continuous section as proposed by YIN in a report about the activities of the P/T Boundary Working Group. This view is also adopted in the present paper.

The Meishan section consists of 7 quarries on the southern slope of the Meishan Hill (Changxing County, Zejiang Province, South China, Fig. 1) separated by distances of 70 - 400 m. They are named as quarry A, B, C, D (Baoqing quarry, stratotype of the Changxingian Stage), E, F and Z (Zhongxin Dadui quarry). The beds of these quarries have identical thicknesses, facies and fossil content (Fig. 2) and as they are laterally traceable, they have been numbered around the P/T boundary in all quarries in the same manner. The Permian-Triassic Boundary Beds (Transitional Beds) and lowermost Triassic rocks are exposed in all of these quarries, while the exposed part of the Changxing Limestone and of the Lower Triassic beds is different. Quarry D exposes the entire Changxingian and the lowermost Triassic, the other quarries only the middle and upper part of the Changxing Limestone, the Boundary Beds and different parts of the Lower Scythian. Best studied are quarries D and Z and the GSSP should be fixed in one of these two quarries by the Chinese colleagues (see, however, remarks to the general accessibility of Chinese sections in section 1). The large lateral extent of the Meishan section allows the collection of very large samples and also the possibility of finding very rare fossils, such as ammonoids.

WANG (1994) used the first appearance of *H. parvus* morphotype 1 sensu KOZUR (1990a) for definition of the P/T boundary. This form is easily recognisable, often even in broken specimens. However, both morphotypes first appeared at the same level. According to WANG (pers. comm.) both morphotypes have a slightly different range. To avoid nomenclatoral problems, morphotype 1 is herein described as a new subspecies *H. parvus erectus* n.subsp. Following WANG (1994), the P/T boundary can be defined by the first appearance of *H. parvus erectus*, within Bed 27 (Boundary Bed 2, upper Transitional Beds).

3. THE IMPACT OF BIOFACIES ON THE DISTRIBUTION OF *Hindeodus* AND GON-DOLELLIDS NEAR THE P/T BOUNDARY

According to ORCHARD (in KRYSTYN & OR-CHARD, 1996) and ORCHARD (1996), gondolellids (*Neogondolella* s.l. sensu ORCHARD) are more common in offshore, deeper, and/or cooler water marine environments, whereas *Hindeodus* flourished in nearshore, shallower and/or warmer regions. The facies control of gondolellids with respect to the water depth is well known since more than 40 years, whereas the temperature control was only studied in the last years (KOZUR, 1995a). Orchard's remarks in respect to the facies control of gondolellids are in general agreement with former published data, except for the temperature control. There are gondolellids, restricted to warm water pelagic environments, e.g. all ribbed Middle Permian Mesogondolella, such as M. nankingensis (CHING) or M. postserrata (BEHNKEN), and gondolellids that are restricted to cold water of high latitudes and cold bottom-water of low latitudes, such as M. phosphoriensis (YOUNGQUIST, HAWLEY & MIL-LER) and M. siciliensis (KOZUR). This temperature control of Mesogondolella has lead often to stratigraphic misinterpretations especially in areas with cold bottom-water faunas and periodical input of shallowpelagic warm water faunas. As mentioned above, Clarkina shows the same facies dependence. Most Upper Permian species, such as C. orientalis (BAR-SKOV & KOROLEVA), C. subcarinata (SWEET), C. leveni (KOZUR, MOSTLER & PJATAKOVA), C. dicerocarinata (WANG & WANG) preferred warm water pelagic environments or are restricted to such facies. In the contrast, C. cf. carinata (CLARK) is restricted to Upper Permian cold/cool water faunas, such as the Boreal lower Otoceras faunas and the conodont faunas of the undisputed Upper Permian uppermost Chhidru Formation (Salt Range), immediately below the likewise undisputed Upper Permian White Sandstone Member. My study of the material published by SWEET (1970b) has shown that he was correct in determination of *Clarkina* of the *C. carinata* group in these deposits. According to ORCHARD (1996) such faunas have a Triassic character. The C. carinata group (with advanced representatives) had adapted to warm water no earlier than in the I. isarcica Zone. For this reason, the H. parvus Zone of the central and western tropical Tethys has no gondolellids after the disappearance of the Permian warm water species and before the appearance of warm water adapted advanced Clarkina carinata in the I. isarcica Zone. This is especially interesting in continuous pelagic sequences, as in western Sicily, where pelagic graded limestones of both the entire Changxingian and the Lower Triassic I. isarcica Zone yielded very rich Clarkina faunas (mostly with very few Hindeodus), whereas in graded calcarenites of the H. parvus Zone (deposited under the same or a little larger water depth) no single Clarkina was found in a conodont fauna consisting exclusively of H. parvus (this monospecific fauna is rich in specimens). No such temperature control for the distribution of Triassic Neogondolella BENDER & STOPPEL and Paragondolella MOSHER can be observed. But these gondolellids belong to an other stock than the Permian Mesogondolella and the Permian to lowermost Triassic Clarkina, and have evolved from the platformless Neospathodus MOSHER through Chengyuania KOZUR (for Paragondolella, within the lowermost Olenekian) and through Chiosella KOZUR (for Neogondolella, within the lowermost Anisian). The ancestral Neospathodus also shows no obvious temperature dependence.

There is no gondolellid preference for offshore deposits as indicated by ORCHARD (1996). The frequency of gondolellids has its maximum in nearshore deeper water (if such deposits are present) and decreases significantly in offshore deeper water. However, this is rather related to the nutrient supply than to the distance from the shore line. Because nearshore limy sediments are rare compared with offshore pelagic limestones, this relations can be observed only in few places.

The Upper Permian and lowermost Triassic Hindeodus species also have different facies control for different species. H. julfensis (SWEET), H. latidentatus latidentaus (KOZUR, MOSTLER & RAHIMI-YAZD), H. changxingensis WANG and H. altudaensis KOZUR & MOSTLER are restricted to deeper, but warm water environments. They are never found in contemporaneous shallow water facies but are also missing in deep water deposits, if they contain cold bottom-water faunas. Most of these forms are rare and can be regarded as ecologically more restricted species than the common Hindeodus species, as H. typicalis (SWEET), H. latidentatus praeparvus and H. parvus. These latter species (and other Hindeodus species) are ecologically very tolerant and could live in environments beyond the ecologic tolerance boundary of other conodont species. Therefore they are often the only conodont species in shallow water environments, in which gondolellids could not live. However, such species with very broad facies tolerance are rare or missing in faunas with species that were better adapted to a certain facies, e.g. in pelagic faunas that are rich in gondolellids or in shallow water faunas that are rich in Stepanovites KOZUR or Merrillina KOZUR. For this reason, Hindeodus is missing in Stepanovites-rich conodont faunas of Kazanian shallow water deposits of the Russian platform or in shallow water Zechstein limestones with rich Merrillina and Stepanovites faunas despite the fact that in other places similar shallow water deposits contains exclusively Hindeodus of the H. typicalis group.

ORCHARD (1996) regarded oceanic cherts as an example, where "*Neogondolella*" occurs alone. However, as a radiolarian worker I have investigated more than 1000 Permian oceanic radiolarites and red deepsea clays rich in deep water radiolarian faunas. Most of these samples have not yielded conodonts, but some contain exclusively gondolellids as mentioned by ORCHARD (1996). These gondolellid faunas mostly consist of juvenile specimens indicating that these oceanic cherts were deposited under facial conditions near to the ecologic tolerance boundary for gondolellids. Other samples, however, contain only *Hindeodus* of the *H. typicalis* group (both juvenile and adult specimens) and a few samples contain both gondolellids and *Hindeodus*.

The above examples show that the occurrence of *Hindeodus* of the *H. typicalis* group is not controlled by the water depth and by the distance to the coast, but by the presence or absence of better adapted species both

in shallow water and in deep water deposits. The H. typicalis group may be present from very shallow water subtidal to intratidal deposits to offshore deep-sea rocks deposited below the CCD. The dominance or exclusive occurrence of the H. typicalis group in many shallow water deposits do not indicate that it is a shallow-water genus but reflect the fact that this facies is beyond the ecologic tolerance boundary of the most other conodonts (e.g. gondolellids), favouring clearly taxa with a very high facies tolerance. Taxa with such a high facies tolerance, as the H. typicalis group that can be found both in very shallow water deposits (widely distributed at the P/T boundary) and in deep-sea sediments, in oxygen-rich and in anoxic facies (widely distributed at the P/T boundary), in cold water and in warm water deposits (both present at the P/T boundary, and having very different non-hindeodid faunas) are far better suited for definition of any stratigraphic boundary than taxa with restricted facies tolerance, as gondolellids that are present only in pelagic facies (present only in few places in the world near the P/T boundary) and moreover strongly temperate dependent with different species in tropical and high latitude faunas (as the ammonoids).

The ecologic model for the distribution of *Hinde-dous* of the *H. typicalis* group, presented herein, explains well the facies-related distribution of conodonts near the P/T boundary in all conodont-bearing complete boundary sections that is in several sections in conflict with the *Hindeodus/"Neogondolella"* biofacies model presented by ORCHARD (1996).

In Meishan, gondolellids are clearly dominant throughout the Changxing Limestone. Hindeodus is very rare in these beds, among them H. latidentatus latidentatus is present that is adapted to warm, deeper water facies. Within the Permian/Triassic Transitional Beds the gondolellid biofacies changes into a Hindeodus biofacies. According to the model presented by ORCHARD (1996) this would indicate a shallowing within the Transitional Beds compared with the upper Changxing Limestones. However, this is in conflict with the observed geological data because within the uppermost bed of the Changxing Limestone a distinct deepening began that continued during the Transitional Beds. The change from warm water gondolellid to Hindeodus dominated faunas is caused by ecologic stress (apparently a short-lasting cooling in the low latitudes because of the presence of aerosoles; KOZUR, 1989, 1994b) that also caused the disappearance of most of the Permian species in other fossil groups. This ecologic stress favoured the ecologically very tolerant Hindeodus of the H. typicalis group against the gondolellids despite the fact that they are better than Hindeodus adapted to pelagic environments, such as the Transitional Beds.

A similar situation can be observed in Transcaucasia and Central Iran. Gondolellids are clearly dominant in the *Paratirolites* beds. Above the *Paratirolites* beds a distinct deepening is indicated for increasingly clayey sediments that finally changed into a red clay. Despite of this obvious deepening, the warm water gondolellids are suddenly replaced by *Hindeodus* of the *H. typicalis* group contemporaneously with the disapparance of most Permian fossils caused by ecologic stress. The causes are the same as discussed for Meishan. According to Orchard's model, a shallowing would be indicated for this level what is against the geological data.

In Kashmir, the shallow water Zewan Formation yielded only very few conodonts, mostly gondolellids. Hindeodus is dominant in the deep water lower Khunamuh Formation with rich ammonoid, partly gondolellids are even absent; in younger beds gondolellids become dominant against Hindeodus. The latter fact may be related to the general decline of Hindeodus near to its extinction. The dominance of the H. typicalis group in the ammonoid-bearing part of the lower Khunamuh Formation is surely not related to shallow-water facies for these pelagic beds. The reasons for the absence or very rare occurrence of gondolellids of the C. carinata group (common in all other peri-Gondwana pelagic successiosn) in these pelagic beds of the lower Khunamuh Formation are not yet known because gondolellids of the C. carinata group are in general not influenced by the cooling event close to the P/T boundary. However, this fact shows that also in cold water pelagic facies that is generally dominated by gondolellids of the C. carinata group (but Hindeodus of the H. typicalis group is not absent in rich faunas), ecologic stress near the P/T boundary may cause the total disappearance of cold water adapted gondolellids, favouring the occurrence of species of the H. typicalis group that are common in these beds.

In Sicily, uppermost Changxingian graded calcarenites with some fusulinids contain a very rich gondolellid fauna and almost no Hindeodus. In the H. parvus Zone a slight deeping is indicated for shales with a few distal graded calcarenites that contain exclusively H. parvus. The absence of any other conodont species and the clear dominance of juvenile H. parvus (adult specimens are extremely rare) indicate that the ecologic conditions in these deep water anoxic to dysaerobic beds were near the ecologic tolerance boundary for H. parvus and clearly beyond this boundary for any other conodont species. The overlying proximal graded calcarenites with conglomeratic layers indicate a distinct shallowing, but they contain Hindeodus and gondolellids. In this section, the rocks deposited under the greatest water depth contain exclusively Hindeodus, rocks deposited under distinctly shallower water depth contain both Hindeodus and gondolellids and rocks deposited under moderate water depth contain almost exclusively gondolellids indicating that the distribution of Hindeodus of the H. typicalis group is not related to the water depth. The Permian warm water gondolellids are totally replaced by H. parvus because of ecologic stress (see above) near the P/T boundary.

The dominance of gondolellids in the cool water peri-Gondwana *H. parvus* Zone can be explained by the fact that the gondolellids of this level are better adapted to pelagic environments than *Hindeodus* with very broad facies tolerance and the ecologic stress in this level (short-lasting cooling event) has mostly not influenced gondolellids of the *C. carinata* group because they were adapted (and in this time still restricted) to cooler water.

4. SYSTEMATIC PART

Remark: For often described taxa, only the oldest reference for a synonym is given to avoid too long synonymy lists.

Genus Hindeodus REXROAD & FURNISH, 1964

Type species: *Trichonodella imperfecta* REX-ROAD, 1957 (*=Spathognathodus cristulus* YOUNG-QUIST & MILLER, 1949).

Synonym: Anchignathodus SWEET, 1970b.

Remarks: *Hindeodus* displays a seximembrate apparatus with Pa, Pb, M, Sa, Sb and Sc elements. Carboniferous to Middle Permian Pa elements of different *Hindeodus* species are rather similar and partly overlap in their variability. However, the ramiform elements, and partly the Sb elements are different enough to facilitate good species separation in those species in which the Pa element is not very diagnostic for separation from other species.

During the Late Permian Lopingian Series and in the earliest Triassic a rapid evolution of the Pa element in *Hindeodus* and closely related genera occurred that is very important for the definition of the P/T boundary and for the Upper Permian-lowermost Triassic conodont zonation (Figs. 2, 3).

Isarcicella KOZUR (1975) is distinguished from *Hindeodus* by a thickening of the cup that commonly bears one or more denticles, or a denticulated side blade on one or both sides of the cup. Forms with a thickened cup and denticles or lateral secondary blade(s) on one or both sides of the cup are typical *Isarcicella*. Forms without denticles or secondary blade(s) on the cup are tentatively assigned to *Isarcicella*, if the cup is thickened in more than half of its width. If in such forms the thickened part of the cup is narrower than half of the cup width, these forms are assigned to *Hindeodus* (transitional forms to *Isarcicella*).

According to SWEET & CLARK (1981), *Isarcicel-'a* is probably unimembrate (only Pa element). However, rich *Isarcicella* faunas always contain some robust ramiform elements that may belong to an *Isarcicella* apparatus. They are sometimes accompanied also by ramiform elements similar to those of *Hindeodus*. However, the frequency of these latter elements is not proportional to the frequency of the Pa elements of *Isarcicella*, but proportional to the frequency of accompanyng *Hindeodus* Pa elements. A reconstruction of the *Isarcicella* apparatus is not yet possible, because all known *Isarcicella* faunas contain also Pa elements of *Hindeodus* and other conodonts (mainly *Ellisonia*). Therefore it is not known whether the ramiform elements that occur together with *Isarcicella* Pa elements all belong to the accompanying Pa elements of *Hindeodus* and other genera (in this case *Isarcicella* would be unimembrate) or whether *Isarcicella* has an apparatus with robust ramiform elements or an apparatus similar to *Hindeodus*. The latter variant is less probable, because the amount of *Hindeodus*-like ramiform elements is independent from the amount of *Isarcicella* Pa elements but proportional to the amount of accompanying *Hindeodus* Pa elements as mentioned above.

ORCHARD (1996) assigned amongst Hindeodus and its derivatives all species "with a conspicuously elevated cusp, equi-dimentional mid-blade denticles, and abruptly terminated posterior margin" (ORC-HARD, 1996, p. 36) to Isarcicella. Thickened lateral margins of the cup and lateral denticles and nodes he regarded as features that may be present or absent. In this scope, Isarcicella should begin at the base of the Triassic according to ORCHARD (1996). He discussed that H. parvus has a perfect Hindeodus apparatus and pointed out that forms with different platform may have the same apparatus. This is correct, but in the case of Neogondolella and Clarkina he rejected on the same page the genus Clarkina because the apparatus of this genus is not known what is not correct because this apparatus was already described by KOZUR (1990b) as he established this genus. The real problem is that ORCHARD (1996) compared the Hindeodus and Isarcicella apparatuses by using the apparatus of "Isarcicella" parva, a Hindeodus species, and he did not discuss the view of SWEET & CLARK (1981) that the type species of Isarcicella has no ramiform elements. This would be a fundamental difference against all Hindeodus species (including H. parvus with Hindeodus apparatus) that have all a seximembrate apparatus with Pa, Pb, M, Sa, Sb and Sc elements, clearly different from other seximembrate apparatuses. As mentioned above, Isarcicella may have an apparatus, but if it is present, it would consist of robust ramiform elements as in Ellisonia. I agree that conodont genera with very different Pa elements may have the same apparatus as I have shown it in several papers (e.g. KOZUR, 1990b), e.g. for Neospathodus and Neogondolella, but conodont apparatuses with distinctly different apparatuses belong always to different genera, the more in the case of Hindeodus and Isarcicella that were originally separated by differences in the Pa elements. So long no apparatus can be found for I. isarcica, the type species of Isarcicella, we have to follow the view of SWEET & CLARK (1981) that the type species of Isarcicella has no ramiform elements. The tentative assignment of H. parvus to Isarcicella by SWEET (1992) was made under the assumption that H. parvus has also an apparatus without ramiform elements.

The three "constant" features that define according to ORCHARD (1996) the genus *Isarcicella* are all fea-

Series	Stage	Substage	Conodont Zone	
			Chiosella gondolelloides	
Early Triassic = Scythian		Late Olenekian	Neospathodus sosioensis	
			Neospathodus triangularis	
			Neospathodus homeri	
	Olenekian		Icriospathodus collinsoni	
	Glenekian		Neospathodus hungaricus	
		Early Olenekian	Neospathodus waageni - Scythogondolella milleri	
			Neospathodus waageni - Scythogondolella? mosheri	
			Chengyuania nepalensis	
		Gandarian	Neospathodus cristagalli	
			Neospathodus dieneri	N. dieneri Sz.
	Brahmanian			"N." kummeli Sz.
	= "Induan"	Ellesmer.	Clarkina carinata	
			Isarcicella isarcica	
			Hindeodus parvus	

Fig. 3 Early Triassic pelagic conodont zonation and conodont proven interval in the sections 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily.

- Conodont-proven in sections 1 or 2 by autochthonous faunas.

Conodont-proven only by reworked faunas. 2

- Conodont faunas of unproven age.

tures that can be observed repeatedly in different Carboniferous and Permian Hindeodus lineages. A conspicuously elevated cusp is present in some Carboniferous and Permian species and the size of the cusp is in some species a variable feature. Equi-dimentional midblade denticles are common in several Permian species, and an abruptly terminated posterior margin is very characteristic for some Middle Permian Hindeodus species. I tend to separate specimens with and without the latter feature as different species or subspecies, but WARDLAW (pers. comm.), who has the greatest experience in Middle Permian Hindeodus, assumes that this feature may represent only intraspecific variability (morphotypes) and this opinion may be correct. In any case, if the three above mentioned features without the thickening of the cusp are taken as the decisive features of Isarcicella, then this genus begins at least in the Middle Permian.

On the other hand, the thickened inner part of the platform is the most important taxonomic feature that never occurs in the Hindeodus stock before the latest Permian. It is the decisive feature present in all typical Isarcicella, including the type species and in all species that are tentatively assigned to Isarcicella, as I.? turgida (KOZUR, MOSTLER & RAHIMI-YAZD). Therefore, it is not understandable, why ORCHARD (1996) wrote that this feature may be present or missing in Isarcicella. Among all species that ORCHARD assigned to *Isarcicella*, it is only missing in *H. parvus* with a typical Hindeodus apparatus, confirming the view that H. parvus does not belong to Isarcicella, but to Hindeodus. H. parvus is the ancestor of H. postparvus, as demonstrated by transitional forms. This species has neither equi-dimentional mid-blade denticles, nor an abruptly terminated posterior margin. In some specimens the cusp is not conspicuously elevated. An abruptly terminated posterior margin is even not present in the holotype of *H. parvus*. If we would use the three "constant" criteria for Isarcicella sensu ORCHARD (1996) for separation from Hindeodus, then "Isarcicella" parva would evolve from Hindeodus (also in the sense of ORCHARD) and its successor would be again a Hindeodus.

The oldest species with thickened inner platform is I.? prisca KOZUR from uppermost Changxingian beds of the Southern Alps that contain Palaeofusulina, Permian brachiopods, H. latidentatus praeparvus and Stepanovites, but no H. parvus. Thus, the Isarcicella lineage began within the uppermost Permian. This oldest representative of the Isarcicella stock has, however, neither a conspicuously elevated cusp, nor equi-dimentional mid-blade denticles, nor an abruptly terminated posterior margin. As in the ancestral genus Hindeodus, these three features are not present in all Isarcicella species.

There is, of course, a possibility to separate species with thickened cup, but without side denticles as an independent genus and to restrict Isarcicella to forms with side denticles or secondary blade on the thickened cup. This possibility cannot be excluded so long the apparatuses of these two groups within Isarcicella cannot be reconstructed. However, also in this case, H. *parvus* would remain a *Hindeodus*, because it has no thickened cup.

The Upper Permian to Lower Triassic species of the *H. typicalis* group (including *H. parvus*) collectively have some apparatus features that are different from the type *Hindeodus* apparatus and from other pre-Permian *Hindeodus* apparatuses. They may be perhaps separated from *Hindeodus* sensu stricto using again the genus *Anchignathodus* SWEET. But for this consideration the apparatus of the *Hindeodus* type species must be restudied. The differences between *Anchignathodus* and *Isarcicella* would be the same as discussed for the differences between *Hindeodus* and *Isarcicella*.

Hindeodus typicalis (SWEET, 1970)

(Pl. I, Figs. 1-8; Pl. IV, Fig. 1)

- 1970a Anchignathodus typicalis n.sp. SWEET, p. 7-8, type material figured in SWEET (1970b), Pl. 1, Figs. 13, 20
- 1970a *Ellisonia teicherti* n.sp. SWEET, p. 8, 9, type material figured in SWEET (1970b), Pl. 4, Figs. 20-28
- 1977 Hindeodus typicalis (SWEET) SWEET, p. 223, Hindeodus - Pl. 2, Figs. 1-6
- 1987 Hindeodus julfensis (SWEET, 1973), pars -NESTELL & WARDLAW, p. 761-767, only Figs. 4.3, 4.6, 4.11, 4.12

Description: The Pa element is rather long and bears in adults nine to fifteen, but commonly ten to twelve denticles. They decrease in length slowly and more or less gradually away from the cusp, which is considerably broader, but only somewhat longer than the denticles on the blade. The upper edge of the denticles is directed slightly downward away from the cusp; but in the posterior third of the unit either a gradual or an abrupt downward curvature is present. There is no distinctly elevated convex hump in the blade. The tips of the denticles are always free. The cup is large, but not thickened.

The ramiform elements are described and figured in SWEET (1970b) under *Ellisonia teicherti* SWEET. The Sb element is especially characteristic. It has a relatively low bar that bears a very large distal or subdistal denticle on the inward curved part of the anterior bar. A short posterior part of the anterior bar is not curved inward. This part bears one to three small denticles.

Occurrence: Upper Permian, world-wide. In the Boreal realm and in peri-Gondwana Tethys also in the lowermost Triassic, but these latter representatives have slight form differences (e.g. a higher bar and/or differences in the denticulation) in some of their ramiform elements and may represent an independent taxon with inseparable Pa elements.

Remarks: The Pa element of *Hindeodus typicalis* (SWEET) is very similar to that of several Carboniferous and Permian species, e.g. *H. minutus* (ELLISON,

1941) to which *H. typicalis* was previously assigned by most authors. However, the Pa element of *H. minutus* generally displays a larger "anticusp", commonly with 1-3 denticles that form a rudimentary anterior blade. Shape of the Pa elements of both species however do overlap. The Sb element of *H. minutus* is distinctly different. Only the distal part of the anterior bar is curved inward and the big distal denticle is missing, as in all other Carboniferous to Middle Permian *Hindeodus* species.

In *H. latidentatus latidentatus* (KOZUR, MOST-LER & RAHIMI-YAZD, 1975), the length of the posterior blade of the Pa element is reduced, the denticles are wider separated and the wide space between the last two denticles is through-like and not triangular as the narrower space between the last two denticles of *H. typicalis*.

In H. latidentatus praeparvus n.subsp. the length of the posterior blade of the Pa element is also reduced. Adults have 5-7, rarely 8-9 rather broad, triangular, commonly widely separated denticles. The cusp is either about twice as long as the denticles or somewhat shorter. The ramiform elements of H. typicalis and H. latidentatus praeparvus are similar, but the bars of the Sb and Sc elements in H. latidentatus praeparvus are distinctly shorter. As they are of the same height, their 1/h ratio is considerably smaller. Moreover, inward curvature of the anterior bar of Sb elements begins closer to the cusp, without any denticle on the very short horizontal part between the inward curved part and the cusp. The bar of the Sa element in H. latidentatus praeparvus is considerably higher than in H. typicalis. Rather regular alternations of long and small denticles are present in the posterior part of the anterior bar of the H. latidentatus praeparvus M element, whereas in the M element of *H. typicalis* the length of the denticles alternate irregularly.

The Pa element of H. julfensis (SWEET, 1973) displays a distinct, convex, mostly smooth hump in the middle third of the posterior blade (Pl. I, Fig. 9). The cusp is distinctly longer than the following denticles. In juvenile forms and in transitional forms between H. typicalis and H. julfensis (H. julfensis wardlawi n.subsp.) the hump bears separated denticles. Such typical Permian forms are still present in the Boreal Otoceras faunas (SWEET, 1976, Pl. 16, Fig. 9 from the Otoceras boreale Zone of Greenland). Forms with a slightly curved upper edge in the posterior half of the blade, but without a distinct hump were also assigned to H. julfensis by NESTELL & WARDLAW (1987), but are herein assigned to H. typicalis. This assignment is supported by the accompanying ramiform elements, which are identical with those of H. typicalis. In contrast, the ramiform elements of H. julfensis (figured by Sweet as Ellisonia teicherti in TEICHERT et al., 1973) are nearly identical with those of *H. latidentatus praeparvus* (higher bar in the Sa element, beginning of the inward curved part of the anterior bar of the Sb element immediately in front of the cusp).

Hindeodus julfensis (SWEET, 1973) (Pl. I, Fig. 9)

- 1973 Anchignathodus julfensis n.sp. SWEET in TEICHERT et al., p. 426-427, Pl. 11, Figs. 10-14
- 1973 Ellisonia teicherti SWEET SWEET in TEI-CHERT et al., p. 433-434, Pl. 12, Figs. 1-5
- 1976 Anchignathodus typicalis SWEET, pars -SWEET, Pl. 16, Fig. 9
- 1987 *Hindeodus julfensis* (SWEET), pars NESTELL & WARDLAW, p. 761-767, only Figs. 4.1 (n.subsp.), 4.2 (n.subsp.), 4.5 (n.subsp.), 4.9, 4.10 (n.subsp.)

Occurrence: Typical *H. julfensis* with a convex smooth hump in adults occurs in the upper Dzhulfian (very rare) and lower to middle Changxingian (in the central Tethys common, but only in warm water pelagic beds). The view of ORCHARD (1996, p. 38) that "*Hindeodus julfensis* sensu stricto is a Dzhulfian species" cannot be confirmed. The holotype and all other specimens of *H. julfensis* published in the original description by Sweet in TEICHERT et al. (1973) were derived from the type Dorashamian (= Changxingian) of Julfa and they occur together with *Clarkina subcarinata* (SWEET), the index species of the Changxingian.

Remarks: *H. julfensis julfensis* is restricted to forms in which the Pa elements of adults display a distinct smooth hump. Pa elements of adults with distinct, but denticulated hump are separated as a new subspecies *H. julfensis wardlawi* n.subsp. Moreover, the Sb elements of the two subspecies are different. In *H. julfensis wardlawi*, one to three small denticles are present on the horizontal posterior part of the anterior bar immediately in front of the cusp, whereas in *H. julfensis julfensis this* part is adenticulated.

Differences between *H. julfensis* and *H. typicalis* have been considered under *H. typicalis*.

H. latidentatus praeparvus n.subsp. is closely related to *H. julfensis wardlawi*, but the Pa element displays fewer denticles and no distinct hump, and the inward curved part of the anterior bar of the Sb element begins immediately in front of the cusp. The ramiform elements of *H. julfensis julfensis* and *H. latidentatus praeparvus* are nearly identical. Only the denticulation of the posterior bar of the Sb element is a little different; in *H. julfensis julfensis* the differences between the large denticles on the posterior portion of the posterior bar and the smaller denticles on its anterior portion are not so strong as in *H. latidentatus praeparvus*, and the length of the denticles of the posterior bar is more irregular.

Hindeodus changxingensis WANG, 1995 from the uppermost Changxingian to lowermost Triassic Boundary Bed 2 at Meishan (South China) has a straight, horizontal, rarely even backwards rising part with fused denticles that comprises the hump and the largest part

of the blade between the hump and the cusp. Only one to four denticles are free between the cusp and the part with fused denticles (in *H. julfensis julfensis* 5-7, rarely 4 denticles with free tips are present in this segment of the blade). Moreover, the cusp is larger in *H. changxingensis* (at least three times longer then the following free denticles on the blade). The posterior part of the blade behind the portion with fused denticles is commonly longer and not so steeply dipping in *H. changxingensis*.

The undenticulated part of the blade in *Hindeodus* altudaensis KOZUR & MOSTLER, 1995 is directed obliquely downward like the denticulated upper edge of the blade. Moreover, the cusp is only slightly longer than the following denticles.

Hindeodus julfensis wardlawi n.subsp.

- 1975 Anchignathodus minutus (ELLISON), pars -KOZUR, MOSTLER & RAHIMI-YAZD, p. 3, only the specimen on Pl. 1, Fig. 11
- 1976 Anchignathodus typicalis SWEET, 1970, reminiscent of A. julfensis SWEET, 1973 SWEET, Pl. 16, Fig. 9
- 1987 Hindeodus julfensis (SWEET, 1973), pars -NESTELL & WARDLAW, p. 761-767, only Figs. 4.1, 4.2, 4.5, 4.10

Derivation of name: In honour of Dr. B. WARD-LAW, Reston, for his outstanding work on Permian conodonts.

Holotype: The specimen figured by NESTELL & WARDLAW, Fig. 4.5.

Locus typicus: Hydra island (Greece), locality 9599 according NESTELL & WARDLAW (1987).

Stratum typicum: Upper Wuchiapingian limestone with *Clarkina orientalis* (BARSKOV & KOROLEVA).

Diagnosis: The Pa element displays a distinct, but denticulated hump. The Sb element bears one to three small denticles on the horizontal posterior part of the anterior bar.

Description: The Pa element displays a distinct cusp, that is two to three times longer and considerably broader than the nine to thirteen small denticles of the blade. The upper edge of the denticles is slightly inclined in its anterior part, then horizontal and a strong downward curvature is present in the posterior third. At the beginning of this downward curvature a distinct, convex, denticulated hump is present, in which the inclination of the denticles becomes rapidly stronger; the last denticle of the blade may be directed backward. The cup is wide, but not thickened.

The ramiform elements are typical for Upper Permian *Hindeodus*. They are well described in NESTELL & WARDLAW (1987, p. 763, 765); only the taxonomically important Sb element is re-described herein. It has a planar posterior bar with eight small denticles behind the cusp that are only very slightly inclined, followed by two to four stronger inclined denticles. The last denticle is in general small. The cusp is large, nearly erect. The short planar posterior part of the anterior bar bears one to three small denticles. The remaining part of the anterior bar is directed inward. It bears several small, and distally or subdistally one large denticle.

Occurrence: Upper Dzhulfian, rarely in the Changxingian.

Remarks: *H. julfensis wardlawi* is transitional between *Hindeodus typicalis* (SWEET, 1970b) and *H. julfensis* (SWEET, 1973). In *H. typicalis*, the cusp of the Pa element is smaller and the upper edge of the denticles is directed downward on the entire blade, whereas in *H. julfensis wardlawi* the upper edge of the denticles is horizontal in the middle part of the blade. The ramiform elements of *H. typicalis* are similar to those of *H. julfensis wardlawi*, but the bar in the Sa element is lower and directed more downward in *H. typicalis*.

The hump in the Pa element of *H. julfensis julfensis* is always smooth in adult specimens. In juvenile specimens (e.g. SWEET in TEICHERT et al., 1973, Pl. 11, Fig. 10), it may be denticulated and such forms are (except for their smaller size) inseparable from the Pa element of *H. julfensis wardlawi*. However, the Sb element of *H. julfensis julfensis* is different. It is shorter, higher and the very short, not inward inclined posterior part of the anterior bar bears no denticles. Moreover, the bar of all ramiform elements in *H. julfensis julfensis* (figured by SWEET in TEICHERT et al., 1973 as *Ellisonia teicherti*) is higher and above all the length:height ratio is considerably smaller.

Hindeodus latidentatus (KOZUR, MOSTLER & RAHIMI-YAZD, 1975) has no hump. In the Pa element of *H. latidentatus praeparvus* n.subsp., the denticles of the blade are larger, their number is smaller and their size is commonly more differentiated (small and slender behind the cusp, larger and above all broader in the posterior half of the blade), but there are also forms, in which the all denticles except the cusp have nearly the same size. The Pa element of *H. latidentatus latidentatus* is additionally distinguished by the widely separated, broader denticles. In the Sb element of *H. latidentatus praeparvus*, there are no denticles between the cusp and the immediately following inward-curved part of the anterior bar.

Hindeodus latidentatus (KOZUR, MOSTLER & RAHIMI-YAZD, 1975)

(Pl. I, Figs. 10, 11; Pl. II, Figs. 1-4)

- 1970a Anchignathodus typicalis n.sp., pars SWEET, p. 7-8, Pl. 1, Fig. 22
- 1970a *Ellisonia teicherti* SWEET, n.sp. SWEET, Pl. 1, Figs. 3, ?8
- 1975 Anchignathodus latidentatus n.sp. KOZUR, MOSTLER & RAHIMI-YAZD, p. 4-5, Pl. 2, Fig. 6

- 1976 Anchignathodus typicalis SWEET, pars -SWEET, only the specimen on Pl. 16, Fig. 7
- ?1979 Anchignathodus parvus KOZUR & PJATAKO-VA - WANG & WANG, p. 116, Pl. 1, Fig. 20
- 1981 *Hindeodus minutus* (ELLISON, 1941), pars -MATSUDA, p. 78-91, Pl. 1, Figs. 1, ?3, 4, 6, 9, 12; Pl. 2, Figs. 1, 5- 7, 11; Pl. 3, Figs. 1-3, 5-7, 10; Pl. 4, Figs. 2, 4, 7, 11, 12
- 1985 Hindeodus latidentatus KOZUR, p. 238
- 1987 Hindeodus typicalis (SWEET, 1970), pars -PERRI & ANDRAGHETTI, p. 308-309, Pl. 32, Fig. 3
- 1991 *Hindeodus typicalis* (SWEET, 1970), pars -PERRI, p. 40-42, Pl. 3, Figs. 2, 5
- 1991 *Hindeodus* cf. *latidentatus* (KOZUR, MOST-LER & RAHIMI-YAZD) - SCHÖNLAUB, Pl. 1, Fig. 9
- 1991 Hindeodus parvus (KOZUR & PJATAKOVA, 1975) pars - SCHÖNLAUB, only Pl. 1, Figs. ?8, ?13
- 1994 *Hindeodus latidentatus* KOZUR, MOSTLER & RAHIMI-YAZD ORCHARD et al., p. 836, Pl. 1, Fig. 20
- 1996 *Hindeodus "latidentatus"* (KOZUR, MOSTLER and RAHIMI-YAZD), 1975, pars - MEI, p. 146, only Pl. 2, Fig. 5
- 1996 *Hindeodus typicalis* (SWEET, 1970), morphotype 1 - MEI, p. 146, Pl. 2, Figs. 8, 9

Occurrence: Upper Changxingian and lowermost Triassic, worldwide.

Remarks: The holotype of *H. latidentatus* represents a rare form with widely separated denticles, in which the last two large denticles are separated by through-like spaces. In 1984 I had prepared a manuscript describing morphologic transitional forms between H. typicalis and H. parvus as a new species H. praeparvus. During finishing that manuscript, I found transitional forms between this assumed new species and H. latidentatus. As I could not definitely separate these two taxa in that time, I used H. latidentatus in an emended sense to include the morphologic transitional forms between H. typicalis and H. parvus. During a long written and personal discussion with Dr. M. ORCHARD, Vancouver, we agreed that both forms are independent taxa that may be separated despite the presence of transitional forms throughout the range of both taxa. Because of the presence of these transitional forms and the fact that their spatial separation is rather facies-controlled, I separated the morphotype praeparvus only as subspecies that corresponds roughly to Hindeodus n.sp. X sensu ORCHARD (1996). Dr. ORCHARD insisted that I should publish this taxon alone.

According to ORCHARD (1996), *H. latidentatus latidentatus (H. latidentatus* sensu ORCHARD) has a different range (upper Changxingian) from *H. latiden-*

tatus praeparvus (Hindeodus n.sp. X sensu ORCH-ARD) that he restricted to the lowermost Triassic. However, these range differences are largely faciescontrolled. H. latidentatus latidentatus is restricted to warm water pelagic deposits, in which H. latidentatus praeparvus is very rare. However, both taxa are present in the upper Changxing Limestone, even the rare morphotype 1 of H. latidentatus praeparvus (MEI, 1996, Pl. 2, Figs. 5, 9) occurs. On the other hand, the holotype of H. latidentatus latidentatus was derived from the lower part of the Transitional Beds in the Iran that has the same fauna as the lower Transitional Beds in South China. According to ORCHARD (1996) the lower Transitional Beds of South China have Triassic character, but are assigned herein (in agreement with most workers) to the uppermost Changxingian because H. parvus, the index species of the lowermost Triassic, evolved only in the middle part of Transitional Bed 2, and the lower Transitional Beds contain typical Permian ammonoid, brachiopod and conodont taxa. H. latidentatus latidentatus is absent in the upper Transitional Beds (with first H. parvus) both in South China and in Iran, whereas H. latidentatus praeparvus continues in these beds with decreasing frequency, but is no longer present above the lower range of H. parvus. These slight differences in upper range may be caused by the low number of H. latidentatus latidentatus even in the time of the maximum frequency of H. latidentatus.

The relations of *H. latidentatus* to other taxa will be discussed under the subspecies.

Hindeodus latidentatus latidentatus KOZUR, MOSTLER & RAHIMI-YAZD, 1975

- 1975 Anchignathodus latidentatus n.sp. KOZUR, MOSTLER & RAHIMI-YAZD, p. 4-5, Pl. 2, Fig. 6
- 1985 Hindeodus latidentatus, pars KOZUR, p. 238
- 1994 Hindeodus latidentatus KOZUR, MOSTLER & RAHIMI-YAZD - ORCHARD et al., p. 836, Pl. 1, Fig. 20
- 1996 *Hindeodus "latidentatus"* (KOZUR, MOSTLER and RAHIMI-YAZD), pars - MEI, p. 146, only Pl. 2, Fig. 5
- 1996 *Hindeodus typicalis* (SWEET), pars YIN & ZHANG, only the specimen on Pl. 8, Fig. 4

Description: Only the Pa element is known. The cusp is large, slender triangular, about twice as long as the denticles on the blade. The length of the denticles increases a little in posterior direction, only the last denticle is mainly short. Two or three denticles adjacent to the cusp are slender, densely spaced with V-shaped spaces between these denticles. The following three denticles are triangular and often very broad. The distance between the posterior three denticles (if a very small last denticle is present) or between the posterior two denticles (if no very small last denticle is present) is very large and the space between these denticle is U-

shaped. The basal cavity is expanded and comprises the entire lower side of the blade. Only below the cusp a broad basal furrow is present.

Occurrence: Upper Changxingian (including lower Transitional Beds) of northwestern and central Iran, Azerbaidzhan-Transcaucasia and South China. Always rare. Restricted to warm water pelagic facies.

Remarks: The above description corresponds to the original scope of the species. Later, the rare and apparently facially restricted H. latidentatus latidentatus was regarded as an extreme variant of the world-wide distributed and common morphologic transitional forms between H. typicalis and H. parvus. All H. latidentatus figured after KOZUR et al. (1975) were in reality these transitional forms, herein described as H. latidentatus praeparvus n.sp. Only ORCHARD et al. (1994), MEI (1996) and YIN & ZHANG (1996) figured again a H. latidentatus sensu stricto from the Meishan section of South China. ORCHARD et al. (1994) recognized that this species has not a big variability including also the ancestors of H. parvus, but also the Chinese forms have the denticulation type of the northwestern Iranian/Transcaucasian type material. Moreover, they recognized that this species in its original scope is restricted to the Upper Changxingian. However, they assumed that H. latidentatus latidentatus is restricted to the upper Changxing Limestone of South China and the timeequivalent Paratirolites Beds of Iran. However, H. latidentatus latidentatus is also present in the lower Transitional Beds of both areas, and also the holotype was derived from this stratigraphic level.

MEI (1996) regarded H. latidentatus s.str. (= H. latidentatus latidentatus) as rare morphotypes of both H. typicalis and H. parvus. However, H. latidentatus latidentatus does not occur together with H. parvus, and consequently cannot be a rare morphotype of H. parvus. The specimen from the H. parvus Zone of Selong that MEI (1996, Pl. 2, Fig. 7) figured under H. "latidentatus" is one of those lowermost Triassic forms assigned in previous papers to H. typicalis that belong to new taxa. Its denticulation (the largest denticles are situated immediately behind the cusp) is totally different from both H. latidentatus and H. typicalis. According to its denticulation, H. latidentatus latidentatus can be only a rare morphotype (restricted to pelagic warm water deposits) of H. latidentatus postparvus, as I have assumed for many years. But such facially and partly also geographically separated morphotypes can be regarded as different subspecies as in the present paper.

YIN & ZHANG (1996) assigned a specimen of H. latidentatus latidentus to H. typicalis (SWEET), but the wide, U-shaped spaces between the large last three denticles are never present in H. typicalis.

Hindeodus latidentatus praeparvus n.subsp. has a variable denticulation. Commonly, it has the same succession of the denticles on the blade as in *H. latidentatus latidentatus* with two, rarely three smaller and above all slender, closely spaced denticles followed by

bigger and above all broader denticles with wider interdenticle spaces, commonly followed by a small denticle. However, the inter-denticle spaces between the last three denticles are V-shaped. Exceptionally the space between the last two denticles may be U-shaped. These forms may be transitional forms to *H. latidentatus latidentatus*, but this feature occurs sometimes also in *H. parvus*.

Hindeodus latidentatus praeparvus n.subsp. (Pl. I, Figs. 10, 11; Pl. II, Figs. 1-4)

- 1970a Anchignathodus typicalis n.sp., pars SWEET, p. 7-8, Pl. 1, Fig. 22
- 1970a *Ellisonia teicherti* SWEET, n.sp. SWEET, Pl. 1, Figs. 3, ?8
- 1976 Anchignathodus typicalis SWEET, pars -SWEET, only the specimen on Pl. 16, Fig. 7
- 21979 Anchignathodus parvus KOZUR & PJATAKO-VA - WANG & WANG, p. 116, Pl. 1, Fig. 20
- 1981 *Hindeodus minutus* (ELLISON, 1941), pars -MATSUDA, p. 78-91, Pl. 1, Figs. 1, ?3, 4, 6, 9, 12; Pl. 2, Figs. 1, 5-7, 11; Pl. 3, Figs. 1-3, 5-7, 10; Pl. 4, Figs. 2, 4, 7, 11, 12
- 1985 Hindeodus latidentatus, pars KOZUR, p. 238
- 1987 Hindeodus typicalis (SWEET, 1970), pars -PERRI & ANDRAGHETTI, p. 308-309, Pl. 32, Fig. 3
- 1991 *Hindeodus typicalis* (SWEET, 1970), pars -PERRI, p. 40-42; Pl. 3, Figs. 2, 5
- 1991 *Hindeodus* cf. *latidentatus* (KOZUR, MOST-LER & RAHIMI-YAZD) - SCHÖNLAUB, Pl. 1, Fig. 9
- 1991 Hindeodus parvus (KOZUR & PJATAKOVA, 1975), pars - SCHÖNLAUB, only Pl. 1, Figs. 28, 213
- 1995b Hindeodus latidentatus (KOZUR, MOSTLER & RAHIMI-YAZD) - KOZUR, p. 67-69, Pl. 1, Fig. 5-8; Pl. 2, Figs. 2, 3
- 1996 *Hindeodus "latidentatus"* (KOZUR, MOSTLER and RAHIMI-YAZD), 1975, pars - MEI, p. 146, only Pl. 2, Fig. 5
- 1996 *Hindeodus typicalis* (SWEET), 1970, morphotype 1 - MEI, p. 146, Pl. 2, Figs. 8, 9

Derivation of name: Assumed ancestor of *H. parvus*.

Holotype: The specimen on Pl. II, Fig. 2, rep.-no. Ko 9003, rep.-no. Ko 8992.

Type locality: Tesero (Southern Alps, Italy), type locality of the Tesero Oolite.

Type stratum: Tesero Oolite, 1.5 m above the Bellerophon Limestone, 0.5 m below the horizon with Changxingian brachiopods, upper Changxingian.

Diagnosis: The Pa element is rather small and bears commonly five to seven denticles that have all approxi-

mately the same length (except a commonly present small denticle at the end of the blade), but two to three denticles behind the cusp are commonly more slender than the broad denticles in the posterior half of the blade. But the denticles may have the same size on the entire blade. The spaces between the denticles are Vshaped, only exceptionally U-shaped between the two last denticles. The cusp is broader and considerably longer than the following denticles (commonly around twice that of the denticles on the blade). The cup is wide, but not thickened. Two morphotypes are present distinguished in denticulation and the height of the posterior end.

Description: The apparatus is seximembrate. The Pa element is relatively short and bears five to seven, rarely eight to nine triangular, mostly broad denticles that are often widely separated. In the rare morphotype 1 the denticles are approximately of equal length and width, relatively narrow, straight or slightly and uniformly inclined, and the very high posterior end of the posterior blade is undenticulated. In the common morphotype 2, the denticles are broadly triangular, widely separated, almost of equal length, but the first two-three denticles after the cusp are commonly distinctly narrower and closer spaced. Sometimes, all denticles are of nearly the same shape and the space between them does not change in the entire blade. The denticulation reaches close to the low or moderately high posterior end of the blade. Both morphotypes are connected by transitional forms, in which all the aforementioned features may be transitional. In both morphotypes the spaces between the denticles are V-shaped. Very rarely the space between the last two denticles is U-shaped. The cusp in both morphotypes is broader and considerably longer than the following denticles (commonly around twice that of the denticles on the posterior blade). The cusp and the denticles are striated. The cup is wide, but not thickened.

The ramiform elements (Pb, M, Sa, Sb, Sc) are figured and described by MATSUDA (1981) under *Hindeodus minutus* (ELLISON, 1941), see synonymy list. They are similar to those of *H. typicalis*, but the bar of the Sa element is higher. The anterior bar of the Sb element immediately in front of the cusp is strongly curved inward. There are no denticles between the cusp and the inward curved part of the bar. The posterior bar is high and bears three to five large denticles in the posterior half and three to four small denticles in the anterior half.

Occurrence: World-wide distributed in the uppermost Changxingian, rarely also in the lowermost Triassic.

Remarks: The ancestor of *Hindeodus latidentatus* praeparvus n.subsp. is either *H. julfensis wardlawi* n.subsp. or a representative of *H. typicalis* (SWEET, 1970b) with somewhat larger cusp. *H. latidentatus* praeparvus and *H. julfensis wardlawi* both display a large cusp on the Pa element and the ramiform elements (except the Sb element) are nearly identical. Only the

Sb element of *H. julfensis wardlawi* is more similar to that of *H. typicalis* because the short horizontal posterior part of the anterior bar displays 1-3 small denticles and the posterior bar displays 10-13 denticles, from which the last 5 denticles are not so large as in the Sb element of *H. latidentatus praeparvus*.

In *H. typicalis* (SWEET, 1970b) (forms with somewhat larger cusp), the Pa element has more denticles (9-15) that are generally more slender and not so widely separated as in morphotype 2 of *H. latidentatus*, and not so uniform in length as in morphotype 1 of this species. Additionally, the bar of the Sa element and generally also of the Sc element is lower, and the Sb element displays a short horizontal posterior portion of the anterior bar with 1-3 denticles between the cusp and the inward curved part.

Some authors have considered H. latidentatus praeparvus as well as H. typicalis as synonyms of H. minutus (ELLISON, 1941). However, both have different Pa and Sb elements. In the Sb element of H. minutus only the anterior portion of the anterior bar is curved inward and has no big denticle.

H. latidentatus praeparvus was also sometimes referred to *Hindeodus parvus* (KOZUR & PJATAKO-VA, 1976), e.g. by WANG & WANG (1979) and SCHÖNLAUB (1991). But in *H. parvus* the cusp is considerably longer (more than twice that of the following denticles) and is generally also more slender. The ramiform elements of *H. parvus* are distinguished by shorter and relatively higher bars in all elements (except the Sa element that has already in *H. latidentatus praeparvus* a very high bar); in the Sb element the cusp and generally also one denticle behind the cusp lie on the inward curved part of the unit.

H. latidentatus praeparvus (= Hindeodus n.sp. X sensu ORCHARD, 1996) is the ancestor of Hindeodus parvus. All transitional forms are present between these two species in stratigraphic sequence. ORCHARD (1996) questioned this derivation because the overlapping ranges of these two taxa, but this view is hardly to understand. In all well documented phylomorphogenetic clines of conodonts and in most clines of other microfossils an overlap of different duration between the range of the ancestral and succeeding forms is present, if there is no stratigraphic break or abrupt facies change between the occurrences of these forms. Sometimes the upper range of the ancestral form exceeds even the range of the succeeding form (as for H. typicalis, the ancestral form of the Changxingian-lowermost Triassic hindeodid stock).

H. latidentatus praeparvus is also the forerunner of the uppermost Changxingian *Isarcicella? prisca* KOZUR, 1995a. These two species display the same denticulation of the blade and the same relative size of the cusp with respect to the following denticles on the blade. However, the inner part of the cup in *I.? prisca* is clearly thickened, as in typical *Isarcicella*.

Isarcicella? turgida (KOZUR, MOSTLER & RA-HIMI-YAZD, 1975) from the lowermost Triassic displays a distinctly thickened inner part of the cup of the Pa element and the cusp is distinctly longer than the denticles of the blade (in general more than twice).

Hindeodus parvus (KOZUR & PJATAKOVA, 1976)

(Pl. II, Figs. 5-8; Pl. III, Figs. 1-11; Pl. IV, Figs. 5-7)

- 1964 Spathognathodus isarcicus HUCKRIEDE, 1958, pars - STAESCHE, p. 288-289, only Figs. 60, 61
- 1970a Ellisonia teicherti SWEET, n.sp., pars -SWEET, p. 8, 9, only Pl. 1, Fig. 7
- 1975 Anchignathodus parvus KOZUR & PJATAKO-VA n.sp., pars - KOZUR, p. 7-9, Pl. 1, only Figs. 17, 21, 22
- 1976 Anchignathodus parvus n.sp., pars KOZUR & PJATAKOVA, p. 123-125, only Figs. 1a, b, e, h
- 1977 Isarcicella isarcica (HUCKRIEDE), pars -SWEET in ZIEGLER, p. 229-230, morphotype
 1 in text-figure "Terminology of Isarcicella KOZUR, 1975" at p. 225
- 1981 *Hindeodus parvus* (KOZUR & PJATAKOVA, 1975) MATSUDA, p. 91-93, Pl. 5, Figs. 1-3
- 1981 *Hindeodus minutus* (ELLISON), pars MAT-SUDA, p. 78-91, only Figs. Pl. 1, Figs. 8, 10, 13;
 Pl. 2, Fig. 8; ?Pl. 3, Fig. 4; ?Pl. 4, Fig. 9
- 1992 Isarcicella ?parva (KOZUR & PJATAKOVA) -SWEET, p. 125
- 1995 *Hindeodus latidentatus* (KOZUR, MOSTLER & RAHIMI-YAZD), pars METCALFE, only the specimen on Pl. 2, Fig. 7
- 1996 *Hindeodus parvus* (KOZUR & PJATAKOVA), morphotype 2 - KOZUR et al., p. 206-207, Pl. 1, Fig. a
- 1966 Hindeodus parvus (KOZUR & PJATAKOVA), morphotype 1 - KOZUR et al., p. 206-207, Pl. 1, Figs. b, g

Description: Apparatus seximembrate. The Pa element is small and displays a very big, rather slender, erect or slightly backward inclined or curved cusp. The following four to nine denticles are less than one-half as large as the cusp. In *H. parvus erectus* (= morphotype 1 of *H. parvus*) the denticles are slender, small, erect, and all nearly of the same size. The posterior part of the blade is steeply inclined and either undenticulated or it bears in the upper part a small denticle that is commonly present at least in adult forms. H. parvus parvus (= morphotype 2 of H. parvus) displays erect, but slightly longer denticles, the upper profile is slightly backward inclined. The posterior third of the blade is occupied by three, rarely two small, strongly inclined denticles. Transitions occur between both forms in the lower part of their ranges. The cup varies from moderately wide to wide, but is not thickened.

The ramiform elements (Pb, M, Sa, Sb, Sc) of *H*. *parvus* are typical for *Hindeodus*, but the bars are relatively short and high.

The Pb element displays a very short anterior bar with one or two denticles. The posterior bar is short and very high and bears denticles of irregular size. It shows a slight torsion. The cusp is large, especially broad. The .ower side displays a narrow basal furrow and an elongated, but not very wide basal cavity.

The M element displays a long and very high anterior bar, whereas a posterior bar is missing. The distinctly Inward curved cusp is relatively narrow, moderately long, but not much longer than the longest denticles on the anterior bar. The anterior bar bears in its anterior part twelve to thirteen small, needle-like, densely spaced denticles of approximately the same size. In the posterior part of the anterior bar, the small to moderately long needle-like denticles alternate regularly with long, needle-like denticles. The four segments with three to four small to moderately long denticles between the long denticles are about equal in length. In general five long denticles are present, the first one lies immediately behind the cusp. The lower side is somewhat inverted and below the cusp above the basal cavity distinctly curved upwards. The basal furrow is very narrow and indistinct.

The Sa element is symmetrical and very high. The lateral bars are relatively short and bear only six to seven denticles of irregular size, but beside the cusp there are always one or two small denticles and the penultimate denticle is always large on both side bars. The cusp is relatively small and not much larger than the largest denticles on the side bars. The lower side is distinctly inverted, but a small pit and an indistinct basal furrow are present adjacent to the pit.

In the Sb element the strongly inward-curved part comprises not only the anterior bar or its anterior portion, like in most other *Hindeodus* species, but also the moderately large cusp and sometimes even the first denticle of the posterior bar. The terminal/subterminal denticles of the anterior bar are sometimes not much larger than the remaining denticles, but there are also Sb elements with large denticles on the posterior part of the anterior bar. The posterior bar is high and short and displays very large posterior denticles that are commonly longer and broader than the cusp. The lower side is strongly inverted and displays an indistinct, small pit.

The Sc element has a short, but high, slightly inward and somewhat downward curved anterior bar with two needle-like, small, erect denticles in front of the cusp and a moderately large, terminal denticle that is more strongly forward inclined than backward curved. The cusp is very long, but slender. The posterior bar is high and bears more than twenty, backwards inclined, needle-like denticles of irregularly varying size. The lower side is somewhat inverted and has a very small pit below the cusp that continues into a very narrow basal furrow.

Occurrence: *Hindeodus parvus* and *Isarcicella isarcica* zones of the lowermost Triassic. World-wide.

Remarks: STAESCHE (1964) regarded the Pa element of H. parvus as an undenticulated morphotype of Isarcicella isarcica. KOZUR (1975) and KOZUR & PJATAKOVA (1976) recognized that this form appeared earlier than I. isarcica and established the new species Anchignathodus parvus, which was later assigned to Hindeodus. SWEET (1977) again regarded H. parvus as a morphotype of I. isarcica, and was followed by PERRI & ANDRAGHETTI (1987) and PER-RI (1991). SWEET (1992) subsequently agreed that H. parvus is an independent species, but assigned it to Isarcicella ?parva assuming that H. parvus is unimembrate as I. isarcica. He was followed by ORCHARD (1994, 1996) and ORCHARD et al. (1994). The discovery in Sicily of a rich monospecific fauna containing the entire apparatus of *H. parvus*, has confirmed the view of KOZUR (1977b) that H. parvus has a Hindeodus type apparatus (then assigned to its junior synonym Anchignathodus). This fauna was found in a Permian-Triassic boundary section 350 m south of Pietra dei Saracini (Sosio Valley, Sicily, Italy, see GULLO & KOZUR, 1993) in thin fine-graded limestone intercalations (distal turdidites) within a 2 m thick anoxic clay at the base of the Triassic. All elements have shorter and relatively higher bars than the Carboniferous and most of the Permian Hindeodus species. Otherwise the ramiform elements are similar to those of *H. typicalis*, *H.* latidentatus praeparvus and H. julfensis, but can be mostly distinguished at species level. In the immediate forerunner, *H. latidentatus praeparvus*, some elements (Sa and Sb elements) already have the same high and short type of the bar; the Sb element already has a rather high bar in H. typicalis.

Advanced representatives of H. parvus commonly have 1-3 small denticles at the anterior edge of the cusp that may form a short, low anterior bar. Such forms were described as *Anchignathodus anterodentatus* in DAI & ZHANG (1989), but are considered herein as a subspecies of H. parvus.

H. parvus evolved from H. latidentatus praeparvus n.subsp. by development of a smaller Pa element with bigger cusp and by development of shorter and relatively higher bars in all ramiform elements. The Sa element is also very high in *H. latidentatus praeparvus* and *H.* julfensis, but bears more denticles (9-10 on each side bar). The Sb element of *H. latidentatus praeparvus* is also as high as in H. parvus, but the inward curved part of the anterior bar begins shortly before the cusp that is situated, as the posterior bar, on the planar part of the element. A very impressive phylomorphogenetic lineage can be observed in the Sb elements from H. typicalis to H. parvus. In H. typicalis, the posterior bar and a short posterior part of the anterior bar with three to four denticles is planar and the inward curved part of the anterior bar begins therefore distinctly before the cusp (Pl. I, Fig. 7). In H. latidentatus the inward curved part begins a little before the cusp, but no denticles are present between the cusp and the inward curved part (Pl. I, Fig. 11). In H. parvus not only the anterior bar,

but also the bar below the cusp and commonly also below the anteriormost denticle of the posterior bar are curved inward (Pl. III, Figs. 6, 10).

The Pa element of Hindeodus postparvus KOZUR, 1990 is distinguished from that of H. parvus by the symmetrically arched upper profile of the blade. The denticles are largest in the mid-length region of the blade or somewhat behind it and have strongly divergent inclination. The M element of H. postparvus is distinguished from that of all other *Hindeodus* species by the presence of a denticulated posterior bar. The stratigraphically youngest representatives of H. parvus with very small Pa element (that occur together with H. postparvus) display also a M element with denticulated posterior bar. Alternatively, all apparatuses with denticulated posterior bar of the M element belong to H. postparvus or the apparatuses with a small H. parvus Pa element and a H. postparvus M element belong to a new species, transitional between H. parvus and H. postparvus.

Isarcicella isarcica (HUCKRIEDE, 1958) is distinguished by thickening of the cup and development of a denticle or a secondary blade on one or both sides of the thickened part of the cup. Moreover, *Isarcicella isarcica* displays either an apparatus consisting only of Pa elements or the *Isarcicella isarcica* apparatus contains robust ramiform elements that generally accompany the *Isarcicella* Pa element. In both cases the apparatuses of *H. parvus* and *I. isarcica* are very different.

Three subspecies, *H. parvus parvus*, *H. parvus anterodentatus* and *H. parvus erectus* n.subsp. are discriminated within *H. parvus*.

Hindeodus parvus parvus (KOZUR & PJATAKOVA, 1976)

- (Pl. II, Fig. 7)
- 1975 Anchignathodus parvus KOZUR & PJATAKO-VA n.sp., pars - KOZUR, p. 7-9, Pl. 1, only Fig. 22
- 1976 Anchignathodus parvus n.sp., pars KOZUR & PJATAKOVA, p. 123-125, only Fig. 1 b
- 1981 Hindeodus minutus (ELLISON, 1941), pars -MATSUDA, p. 78-91, Pl. 1, only Fig. 10
- 1981 Hindeodus parvus (KOZUR & PJATAKOVA, 1975), pars - MATSUDA, p. 91-93, Pl. 5, only Fig. 3
- 1990a *Hindeodus parvus* (KOZUR & PJATAKOVA, 1976), morphotype 2 KOZUR, p. 400

Description: See at *H. parvus*. The Pa element is small and bears eight to nine denticles; their upper profile line is somewhat backwards inclined. The posterior steeply inclined high part of the blade bears three, rarely two small denticles. Ramiform elements as for the species.

Occurrence: *H. parvus* Zone to slightly above the *I. isarcica* Zone of lowermost Triassic. *H. parvus parvus* is not as facies tolerant as *H. parvus erectus*. Therefore it is missing in anoxic or dysaerobic beds, in which *H. parvus erectus* is commonly the only present conodont taxon and often the only fossil.

Remarks: *Hindeodus parvus erectus* n.subsp. displays 4-7 denticles with a commonly straight, horizontal upper profile. The steeply dipping to vertical high posterior end is smooth or bears one small denticle (commonly in adult forms).

In *Hindeodus latidentatus praeparvus* n.subsp., the Pa element is larger and the cusp relatively shorter and broader. The denticulation is very similar in many specimens (common morphotype 2 of *H. latidentatus praeparvus*). The ramiform elements are comparable, but longer and except in the Sa and Sb elements the bar is lower. The inward bent of the Sb element begins in front of the cusp that is always situated on the planar part of the bar.

The Pa element of *H. postparvus* KOZUR, 1990 is similar, but the inclination of the denticles is more strongly divergent and their upper profile line is convex. The M element is distinguished by the presence of a denticulated posterior bar.

Hindeodus parvus anterodentatus (DAI, TIAN & ZHANG, 1989) (Pl. IV, Fig. 5)

- 1989 Anchignathodus anterodentatus DAI, TIAN & ZHANG (sp.nov.) DAI & ZHANG, Pl. 45, Figs. 14, 15; non! Pl. 48, Figs. 10, 11
- 1993 Hindeodus anterodentatus DAI & TIAN GUL-LO & KOZUR, Fig. 2.11
- 1995 *Hindeodus parvus* (KOZUR & PJATAKOVA), pars - METCALFE, Pl. 2, Figs. ?3, 4

Occurrence: *Isarcicella isarcica* Zone. Worldwide. *H. parvus anterodentatus* appears at the base of the *I. isarcica* Zone. In the absence of the index species (e.g. in Greenland) the first appearance of *H. parvus anterodentatus* is a suitable marker for the base of the *I. isarcica* Zone.

Remarks: The presence of one to three denticles on the anterior edge of the cusp is mostly without taxonomic importance in Carboniferous and Permian *Hindeodus* species. However, in *H. parvus* this feature occurs only in forms from the *I. isarcica* Zone. Therefore, these forms are regarded as an independent subspecies. As *H. parvus anterodentatus* is always accompanied by other *Hindeodus* species, the ramiform elements of its apparatus cannot be assigned with certainity. They may be comparable with those of the other subspecies of *H. parvus*, but the Sc element may be more advanced (see remarks to *H. postparvus*).

Hindeodus parvus erectus n. subsp.

(Pl. II, Figs. 6, 8; Pl. III, Figs. 1-11; Pl. IV, Figs. 6, 7)

- 1964 Spathognathodus isarcicus HUCKRIEDE, 1958, pars - STAESCHE, 288-289, only Figs. 60, 61
- 1975 Anchignathodus parvus KOZUR & PJATA-KOVA n.sp., pars - KOZUR, p. 7-8, Pl. 1, only Fig. 17
- 1976 Anchignathodus parvus n.sp., pars KOZUR & PJATAKOVA, p. 123-125, only Fig. 1a
- 1981 *Hindeodus minutus* (ELLISON, 1941), pars -MATSUDA, p. 78-91, Pl. 1, Figs. 8, 13
- 1981 *Hindeodus parvus* (KOZUR & PJATAKOVA, 1975) MATSUDA, p. 91-93, Pl. 5, Figs. 1, ?2
- 1990a Hindeodus parvus (KOZUR & PJATAKOVA, 1976), morphotype 1 - KOZUR, p. 400
- 1995 Hindeodus latidentatus (KOZUR, MOSTLER & RAHIMI-YAZD), pars - METCALFE, only the specimen on Pl. 2, Fig. 7

Derivation of name: According to the erect denticles of the blade behind the cusp.

Holotype: The specimen on Pl. II, Fig. 6, rep.-no. 123254, refigured from WANG (1994, Pl. 1, Fig. 1).

Locus typicus: Meishan section (South China), Zhongxin Dadui quarry.

Stratum typicum: Upper part of Boundary Bed 2, sample 882-4 (12-16 cm above the base of Boundary Bed 2), *H. parvus* Zone of lowermost Triassic.

Material: Several hundred specimens.

Diagnosis: *Hindeodus parvus* with slender, small, erect denticles, all nearly of the same size. The commonly high posterior part of the blade is steeply inclined and undenticulated, but in the upper part of this smooth portion a small denticle is commonly present in adult forms.

Description: The Pa element is small, with a very large, slender cusp, more than twice as long as the following denticles. The cup is wide, but not thickened. The blade is short, high, in adults with four to seven erect, small, slender denticles of equal length. The upper edge of the blade is horizontal, straight or nearly so. The posterior part of the blade is (except for a small denticle in adults) smooth, commonly high and steeply dipping. For the ramiform elements see at *H. parvus*.

Occurrence: World-wide guide-form of the lowermost Triassic.

Remarks: The Meishan section is proposed as the GSSP for the base of the Triassic that is defined by the first appearance of *H. parvus* in the upper half of Boundary Bed 2. For this reason, the holotype of *H. parvus erectus* n.subsp. is chosen from the upper half of Boundary Bed 2 of that section. Specimens of this subspecies from other part of the world demonstrate the wide distribution of this taxon.

In Hindeodus parvus parvus (KOZUR & PJATA-KOVA, 1976), the upper profile of the blade behind the large cusp is slightly inclined. The steeply inclined posterior part of the blade bears 2-3 small denticles. Both forms are connected by transitional forms in the lower part of their ranges and have been discriminated as two morphotypes of H. parvus by KOZUR (1990a), morphotype 1 being H. parvus erectus. However, the differences are large enough to distinguish two subspecies. According to Prof. WANG (Nanjing, pers. comm.), both morphotypes have a slightly different range. In our material, different occurrences are rather facies-controlled. The rich fauna of the lowermost Triassic of Sicily consists exclusively of H. parvus erectus, mostly juvenile forms. They have been derived from anoxic to dysaerobic beds deposited under greater water depth. As this fauna consists of numerous specimens in a monospecific fauna, H. parvus erectus could seemingly live near the ecologic tolerance boundary for conodonts. H. parvus parvus and any other conodont species could not live in this facies. H. parvus erectus is also present in shallow-water deposits of the Southern Alps and in pelagic red, bioturbate clays and marls in Transcaucasia. It also occurs in pelagic gray beds with ammonoids and/or gondolellid conodonts in Iran, South China, in peri-Gondwana Kashmir and in Greenland. This universal distribution makes the first appearance of H. parvus erectus an excellent marker for the base of the Triassic. This is in agreement with the opinion of WANG (1994) to use the first appearance of H. parvus morphotype 1 for the definition of the base of Triassic. Its forerunner, connected by transitional forms in stratigraphic sequence in several sections, is H. latidentatus praeparvus n.subsp. It is distinguished by a somewhat larger Pa element with shorter and broader cusp and by the beginning of the inward curved part of the Sb element in front of the cusp.

Hindeodus changxingensis WANG, 1995

(Pl. V, Figs. 1, 2)

- 1994 Hindeodus n.sp. WANG, Pl. 1, Fig. 10
- 1994 Hindeodus julfensis (SWEET, 1973) WANG, Pl. 1, Fig. 11
- 1995b Hindeodus changxingensis sp.nov. WANG, p. 149-150, Pl. 2, Figs. 14-18

Description: The Pa element has a lanceolate, deeply excavated cup. The free blade bears a very broad and long, erect cusp, which is approximately three times longer than the following small denticles on the blade. One to four (mostly one or two) denticles behind the cusp have discrete tips. The tips of the following denticles are fused to a straight or somewhat wavy ridge that is horizontal or nearly horizontal. The posterior end of the fused part dips very steeply, often vertically and only this part may be convex. The following posterior third of the blade bears two to four discrete, broad, but low denticles. The upper profile of this part is gently inclined backwards. Ramiform elements cannot be assigned precisely to this species because it always occurs together with several other *Hindeodus* species.

Occurrence: *Hindeodus changxingensis* WANG is restricted to the uppermost part of the Changxingian and the lowermost 4 cm of the Triassic part of the Boundary Beds at Meishan (South China).

Remarks: *H. changxingensis* was first figured as *Hindeodus* n.sp. by WANG (1994), but not described. The description was published in WANG (1995b). He restricted this species to forms with a long fused, horizontal part of the blade and only one free denticle between the cusp and the fused part of the blade. Forms with three to four free denticles behind the cup and a short, rising backwards fused part of the blade, were assigned to *H. julfensis* (SWEET) by WANG (1994, 1995b). However, these forms are closely related to the type *H. changxingensis* in having a very large cusp, rather few free denticles between the cusp and the fused part of the blade, and an often long, gently backward dipping posterior part of the blade. They are therefore assigned to *H. changxingensis*.

Hindeodus julfensis (SWEET, 1973) has a shorter cusp, more free denticles between the cusp and the portion with fused denticles (five to seven, in advanced forms four) that is always a convex hump, and the portion with free denticles behind the fused part is considerably steeper dipping and mostly shorter.

In *Hindeodus altudaensis* KOZUR & MOSTLER, 1995 the fused part is also straight, but distinctly inclined backwards. The posterior part of the blade behind the portion with fused denticles is strongly inclined, more or less vertical close to the posterior end.

Hindeodus postparvus KOZUR, 1990

(Pl. II, Figs. 9, 10)

- 1958 Spathognathodus cf. minutus (ELLISON) -HUCKRIEDE, p. 162, Pl. 10, Fig. 8
- 1975 Anchignathodus parvus KOZUR & PJATAKO-VA n.sp., pars - KOZUR, p. 7-9, Pl. 1, Figs. 19, 20, non! Figs. 17, 21-23
- 1976 Anchignathodus parvus n.sp., pars KOZUR & PJATAKOVA, p. 123-125, Figs. 1c, d, non! Figs. 1a, b, e, g, h
- 21981 Hindeodus minutus (ELLISON, 1941), pars -MATSUDA, p. 78-91, only Pl. 3, Fig. 10
- 1990a Hindeodus postparvus n.sp. KOZUR, p. 400
- 1995 *Hindeodus julfensis* (TEICHERT, KUMMEL & SWEET) METCALFE, Pl. 2, Fig. 10
- 1995 *Hindeodus latidentatus* (KOZUR, MOSTLER & RAHIMI-YAZD), pars METCALFE, Pl. 2, Fig. 8

Diagnosis: The Pa element is small and arched. It has commonly a large cusp and six to seven, rarely

more, large, highly fused denticles with strongly diverging inclination. One or two, rarely three or four small denticles may be present on the anterior edge of the cusp, forming a reduced anterior blade. The denticles are largest in the mid-length of the blade or somewhat behind it. This size distribution together with the strongly diverging inclination of the denticles results in an distinctly arched upper profile of the Pa element. The cup is large, but not thickened. The M element displays a distinct, denticulated posterior bar, very different from all other *Hindeodus* species. The other ramiform elements are not yet exactly assignable to *H. postparvus*, but except the Sc element they may be all comparable to those of *H. parvus*.

Occurrence: Upper *Ophiceras tibeticum* ammonoid Zone of the lowermost Triassic. The species first occurs in the *I. isarcica* Zone, but its main occurrence lies above this zone.

Remarks: METCALFE (1995) assigned a Pa element of *H. postparvus* to the characteristic Changxingian guide form *H. julfensis* (SWEET). A part of *H.* latidentatus sensu METCALFE (1995) belongs also to H. postparvus (op.cit., Pl. 2, Fig. 8). Other specimens of H. latidentatus sensu METCALFE (1995) belong to H. parvus (op.cit., Pl. 2, Fig. 7) or H. cf. typicalis (op.cit., Pl. 2, Figs. 6, 9). The latter forms are, as H. parvus, typical conodonts of the lowermost Triassic. Formerly, they were assigned mostly to H. typicalis, but are distinguished from this species by the smaller Pa element and irregular denticles of the blade that are often wider separated. The cusp is slender and moderately long. By their slender cusp and irregular denticles they are also distinguished from H. latidentatus praeparvus. These forms will be described as independent taxa in a separate paper because their apparatuses are not yet well known.

As the figured specimens of the Changxingian *Clarkina changxingensis* (WANG & WANG) by MET-CALFE (1995) belong all to the Triassic *Clarkina carînata* (CLARK) sensu stricto and closely related forms, the entire fauna is typical for the *I. isarcica* Zone and the following *H. postparvus* fauna (or zone) and not a mixed fauna of Griesbachian age with reworked Permian elements as assumed by METCALFE (1995).

H. postparvus KOZUR evolved from *H. parvus* parvus (KOZUR & PJATAKOVA) (= *H. parvus*, morphotype 2) by separation of the posterior denticles of the Pa element in size and inclination from the erect anterior denticles. Moreover, in *H. parvus parvus* only the upper profile of the posterior third of the blade is arched, the upper profile of the anterior portion of the blade being horizontal or inclined slightly in the posterior direction. An other difference is the development of a denticulated posterior bar in the M element.

Most of the ramiform elements of *H. postparvus* cannot be correctly assigned to this species because *H. postparvus* always occurs together with other *Hindeo- dus* species. Only the M element with a denticulated

posterior bar can be easily recognized because this feature is missing in all other Hindeodus species. Only very advanced small Pa elements of H. parvus from the H. postparvus Zone may have an apparatus, in which the M element has a denticulated posterior bar. As the development of a posterior bar in the M element is an unique and easily recognizable feature of the Hindeodus apparatus, there may be also other explanations for the occurrence of this feature in very advanced H. parvus apparatuses. Either the intraspecific variabiliy of the Pa element of H. postparvus is high, and parts of the Pa elements cannot be distinguished from those of H. parvus or the development of a posterior bar in the M element begins earlier then the changes of the Pa element and apparatuses with H. parvus Pa element and H. postparvus M element represent transitional forms between both species.

In one sample from Transcaucasia that yielded only *H. postparvus* and *H. parvus anterodentatus*, typical but broken ramiform elements of *Hindeodus* occur. Only the Sc element is rather well preserved and corresponds to the Sc element figured by MATSUDA (1981, Pl. 3, Fig. 10). It displays an inward curved, short and high anterior bar with one very big terminal denticle. The cusp is moderately large, but not larger than the denticle on the anterior bar. The posterior bar displays three to four denticles behind the cusp and three large denticles in the posterior part. This Sc element is more advanced than that of *H. parvus*, but it may belong both to *H. parvus anterodentatus* or to *H. postparvus*.

Hindeodus sosioensis n.sp.

(Pl. IV, Figs. 2-4)

Derivation of name: According to its occurrence in the Sosio Valley, western Sicily.

Holotype: The specimen on Pl. IV, Fig. 2; rep.-no. 4-12-94/VI-14.

Locus typicus: 350 m south of Pietra dei Saracini, 50 m east of the road.

Stratum typicum: Floated block of turbiditic graded calcarenite, earliest Triassic.

Material: 6 specimens.

Diagnosis: The Pa element has a short, but distinct anterior bar and large denticles on the posterior bar, one of them being as large as the prominent cusp. The Sb element is short and high, but between the cusp and the inward curved part of the anterior bar a short, denticulated, horizontal part of the anterior bar is present.

Description: The Pa element is distinctly arched. It has a short anterior bar that bears two small, erect denticles. The cusp is large, nearly erect to inclined slightly backwards. The posterior bar bears around seven large denticles that are inclined slightly backwards. The inclination does not increase significantly towards the posterior end. The size of the denticles is variable, the second one is as long and broad as the cusp. The cup is moderately wide, not thickened.

The Pb element is short and relatively high. Its anterior bar bears three denticles, two of them are rather large. The cusp is large and inclined backwards. The posterior bar bears seven moderately inclined denticles of different size, the largest occurring in the posterior half of the bar. The lower side of the bar is slightly inverted, but an elongated basal cavity and a narrow basal furrow are present.

The Sb element is short and high. The anterior bar is strongly inward-curved, but its posterior part is horizontal and bears four small denticles. The inward curved part bears seven denticles; one or two denticles at its anterior end are very large. The posterior bar has seven denticles of different size, but behind the cusp they are smaller and at the posterior end one or two large denticles are present. The lower side of the bar is strongly inverted.

Occurrence: Lowermost Triassic of Sicily. *Hindeodus sosioensis* n.sp. has been derived from a floated block of graded calcarenites, with *H*. cf. *typicalis* (Pl. IV, Fig. 1) and *Ellisonia transita* KOZUR & MOST-LER. Changxingian *Clarkina* species are missing. In the exposed part, all Scythian calcarenites with *Hindeodus* belong to the *Isarcicella isarcica* Zone. *H.* cf. *typicalis* occurs from the *H. parvus* Zone to the *H. postparvus* fauna (or zone) immediately above the *I. isarcica* Zone.

Remarks: The Pa element is only similar to that of *Hindeodus postparvus* (KOZUR, 1990) which also has an arched Pa element with a large cusp and large denticles on the blade. However, in *H. postparvus* the inclination of the denticles is more divergent and no denticle behind the cusp is as long as the cusp.

Sample KS 2 contains all the ramiform elements of Hindeodus, except the Sa element that is always rare in Hindeodus. However, only the Sb element and the Pb element are different from those in Hindeodus cf. typicalis, the second Hindeodus species that is represented by Pa elements in this sample. For this reason, the Sc and M element of H. sosioensis are either identical with those of H. cf. typicalis or not present in sample PK 2. Sb and Pb elements display some features of H. typicalis (SWEET, 1973) and some features of H. parvus (KOZUR & PJATAKOVA, 1976), but are different from those elements in both species. The Sb element is as high and short as in H. parvus. However, the posterior part of the anterior bar is not inward-curved, horizontal and bears up to four small denticles as in H. typicalis. The Pb element of H. typicalis is longer, above all, the anterior bar is considerably longer, but lower relative to its length. In H. parvus, the anterior bar of the Pb element is shorter (only one denticle) and the entire unit is higher.

Genus Isarcicella KOZUR, 1975

Type species: Spathognathodus isarcicus HUCK-RIEDE, 1958 Occurrence: Uppermost Changxingian and lower two zones of the Triassic, but common only in the *Isarcicella isarcica* Zone.

Remarks: See at *Hindeodus* REXROAD & FUR-NISH, 1964.

Isarcicella isarcica (HUCKRIEDE)

(Pl. V, Figs. 6, 9)

- 1958 Spathognathodus isarcicus n.sp. HUCK-RIEDE, p. 162, Pl. 10, Figs. 6, 7
- 1975 Isarcicella isarcicus (HUCKRIEDE) KOZUR, p. 12
- 1981 Isarcicella isarcica (HUCKRIEDE) MATSU-DA, p. 93-94, textfig. 5, Pl. 5, Figs. 4-7
- 1981 Isarcicella ?sp. MATSUDA, p. 94-95, Pl. 5, Fig. 8
- 1989 Isarcicella staeschei DAI & ZHANG (sp.nov.) DAI & ZHANG, p. 430-431, Pl. 45, Figs. 16, 17; Pl. 46, Figs. 4-7, 11-13, 18, 19; Pl. 53, Figs. 13, 14
- 1989 Isarcicella triangulata DAI & ZHANG (sp.nov.) - DAI & ZHANG, p. 431, Pl. 46, Figs. 8-10, 21

Occurrence: Very rare in the upper *H. parvus* Zone (only *I. isarcica staeschei* DAI & ZHANG). Common in the *I. isarcica* Zone. North America and Tethys, including the peri-Gondwana Tethys margin. Until now unobserved in Greenland.

Remarks: *Isarcicella isarcica* evolved from *I*.? turgida (KOZUR, MOSTLER & RAHIMI-YAZD, 1975) through I. isarcica staeschei DAI & ZHANG, 1989 as transitional forms. The most primitive representatives of Isarcicella s.str. display only one denticle attached to a side of the thickened blade or the blade is bifurcated. Such forms very rarely occur in the H. parvus Zone of the Southern Alps (one specimen reported by PERRI, 1991) and of Kashmir (one specimen from the H. parvus Zone of the upper Otoceras woodwardi Zone, reported by MATSUDA, 1981 as Isarcicella? sp.). As these forms are extremely rare (only one specimen of each type is known so far), it cannot be determined whether they are independent taxa, subspecies of I. isarcica or pathological forms of I.? turgida.

Forms with one or two denticles on one side of the cup dominate throughout the *I. isarcica* Zone, but forms with denticles or a short secondary blade on both sides of the cup also occur there. The holotype of *I. isarcica* belongs to these latter forms. DAI & ZHANG (1989) separated specimens with denticles only on one side as a different species. Unfortunately, they have chosen a form with two denticles on one side of the cup as holotype. Such forms occur exclusively in the *I. isarcica* Zone, as do forms with denticles on both sides of the cup. Only specimens with one denticle on one side of the cup have a different range. It is probably that only these forms represent a different taxon and the

separation proposed by DAI & ZHANG (1989) is an arbitrary one. However, it is possible to use *I. staeschei* as an independent subspecies *I. isarcica staeschei* DAI & ZHANG (Pl. V, Fig. 6).

Isarcicella triangularis DAI & ZHANG, 1989, with triangular platform, is only a morphotype of *I. isarcica* with the same range as the other morphotypes. It is regarded as junior synonym of *I. isarcica*.

Isarcicella? turgida (KOZUR, MOSTLER & RAHIMI-YAZD, 1975)

(Pl. V, Figs. 7, 8)

- 1975 Anchignathodus turgidus n.sp. KOZUR, MOSTLER & RAHIMI-YAZD, p. 5-6, Pl. 7, Figs. 11, 12
- 1989 Anchignathodus decrescens DAI & ZHANG (sp.nov.) - DAI & ZHANG, p. 428, Pl. 39, Figs. 11-13
- 1993 Isarcicella turgida (KOZUR, MOSTLER & RAHIMI-YAZD) GULLO & KOZUR, Figs. 2/7-9
- ?1995 *Hindeodus latidentatus* (KOZUR, MOSTLER & RAHIMI-YAZD) ZHANG et al., Pl. 2, Fig. 12
- 1995 *Hindeodus parvus Isarcicella* Transition ? METCALFE, Pl. 1, Figs. 12, 13
- 1996 Hindeodus parvus, pars MEI, p. 146

Occurrence: Lowermost Triassic *H. parvus* and *I. isarcica* zones. *I.* cf. *turgida* occurs in the uppermost Changxingian.

Remarks: As shown on Pl. V, Fig. 7, the inner part of the cup in *I*.? *turgida* is thickened to form a platform, as in *Isarcicella isarcica*. This is the main difference to *H. parvus*, but additionally *I*.? *turgida* is larger, displays more denticles, and primitive forms from the uppermost Changxingian (*I*.? cf. *turgida*, probably a separate taxon) display a low blade. Unlike *I. isarcica*, the platform of *I*.? *turgida* does not bear a denticle or a secondary blade on one or both sides. However, as these forms already exhibit one of the *Isarcicella* by GUL-LO & KOZUR (1993).

I.? turgida was regarded until now as a transitional form between *H. parvus* and *I. isarcica*. However, *I.?* cf. *turgida* (distinguished by its low blade from typical *I.? turgida*) which is the immediate ancestor of typical *I.? turgida*, first occurs in the uppermost Changxingian, before the first appearance of *H. parvus*. The specimen figured by ZHANG et al. (1995, Pl. 2, Fig. 12, re-figured by YIN & ZHANG, 1996, Pl. II.8, Fig. 11, and by ZHANG et al., 1996, Fig. 5.3) as *H. latidentatus* from Bed 25 of Meishan, perhaps belongs to *I.?* cf. *turgida* but no upper view was figured, and therefore it cannot be decided whether the cup is thickened. If the cup is not thickened, this specimen would be either a *H. latidenatus praeparvus* with unusual large cusp (in this case the original determination would be correct) or

rather a new species. The very large, broad cusp and the low blade of this specimen are characteristic for *I*. cf. *turgida*, but also for some specimens of *H*. *latidentatus praeparvus*. MEI (1996) assigned this specimen to *H*. *parvus* because of its very big cusp, but *H*. *parvus* displays a high blade and not such a broad cusp as in this specimen. *H*. *parvus* and *I*.? *turgida* first appear in the Meishan section in Beds 27 c. A derivation of *I*.? *turgi da* from *H*. *parvus* can be therefore excluded, the more as *H*. *postparvus* evolved from *H*. *parvus*. ORCHARD (1996) assigned *H*. *latidentatus* sensu ZHANG et al. (1995, Pl. 2, Fig. 12) to *Isarcicella* aff. *parva*, but in a written communication he stated that this specimen belongs neither to *H*. *latidentatus* nor to "*I*." *parva*.

Anchignathodus decrescens DAI & ZHANG, 1989 is a junior synonym of *I.? turgida* (KOZUR, MOST-LER & RAHIMI-YAZD, 1975). Also this species is characterized by a thickened inner part of the cup and by a prominent cusp that is more than twice as long as the following denticles. The figured specimens are somewhat smaller and have fewer denticles than adult *I.? turgida*. They are seemingly juvenile specimens.

Isarcicella isarcica (HUCKRIEDE, 1958) displays denticles on the cup. Most primitive representatives of *I. isarcica staeschei* DAI & ZHANG (1989) bear only one denticle on one side of the cup. They are transitional forms between *I.? turgida* and *I. isarcica*.

Isarcicella? prisca KOZUR, 1995a from the uppermost Changxingian displays a denticulation of the blade as in *H. latidentatus* morphotype 2. The cusp is distinctly smaller than in *I.? turgida*.

Isarcicella? prisca KOZUR, 1995a (Pl. IV, Fig. 9)

- 1991 *Hindeodus typicalis* (SWEET), pars PERRI, p. 40, 42, Pl. 3, Figs. 1, 3, 4
- 1995a *Isarcicella? prisca* n.sp. KOZUR, p. 168, Pl. 6, figs. 3, 4

Description: The Pa element is rather small and bears six to nine slightly backward inclined denticles that are largest in the posterior half of the blade. The cusp is considerably broader and somewhat to distinctly larger than the following denticles. The inner part of the cup is distinctly thickened, but the outer, unthickened part is rather broad.

Occurrence: Upper Changxingian Tesero Oolite of Southern Alps. Uppermost Dorashamian of Transcaucasia (only broken specimens) and uppermost Changxingian of South China.

Remarks: The denticulation of the blade and the size of the cusp corresponds to *Hindeodus latidentatus* (KOZUR, MOSTLER & RAHIMI-YAZD, 1975). *1.? prisca* n.sp. is distinguished from *H. latidentatus* by the distinct thickening of the inner part of the cup, typical for all *Isarcicella* species, but the unthickened part of the cup is still rather broad.

Isarcicella? turgida (KOZUR, MOSTLER & RA-

HIMI-YAZD, 1975) from the lowermost Triassic displays a more prominent cusp that is more than twice as long as the following denticles. The thickened part of its cup is wider than in *I.? prisca*, the most primitive *Isarcicella* species.

Genus Sweetohindeodus n.gen.

Type species: Sweetohindeodus bidentatus n.gen. n.sp.

Derivation of name: In honour of Prof. W.C. SWEET, Columbus, for his outstanding contribution to Upper Permian-Lower Triassic *Hindeodus* taxonomy and in gratitude for his help with my conodont studies.

Diagnosis: The cup is large, circular to subcircular. The blade is very short, somewhat thickened on the cup, with a large, erect cusp that is followed by one or two large separated denticles.

Occurrence: *Isarcicella isarcica* Zone (Lower Scythian) of western Sicily.

Assigned species:

Sweetohindeodus bidentatus n.gen. n.sp. Sweetohindeodus tridentatus n.sp.

Remarks: Only the Pa element of *Sweetohindeodus* is known. The short blade with two or three large separated denticles (including the cusp) clearly distinguishes the Pa element of *Sweetohindeodus* from that of its ancestor, *Hindeodus* REXROAD & FURNISH, 1964.

Sweetohindeodus bidentatus n.sp.

(Pl. V, Figs. 3, 4)

Derivation of name: According to the presence of only two large denticles.

Holotype: The specimen figured on Pl. V, Fig. 4; rep.-no. Ko 12-11-91/IX-2.

Locus typicus: Lower Triassic section 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (see Fig. 4).

Stratum typicum: Sample Ko 12 A, uppermost 5 cm of a graded calcarenite of the 2 m thick lower calciturbidites above the lowermost Triassic shales. *Isarcicella isarcica* Zone of Lower Scythian.

Material: 7 specimens.

Diagnosis: The very short blade bears two denticles, a slender, large cusp and a very broad denticle, far broader than and as long as the cusp.

Description: The cup is large, subcircular and at its lower side is deeply excavated. The very short blade bears only two erect denticles. One of them, the cusp, is long and slender; it is situated on the free part of the blade. The other one is very broad, laterally compressed and subconical. In the direction of the blade, the base of this denticle is only a little shorter than the cup. Both denticles may be finely striated.

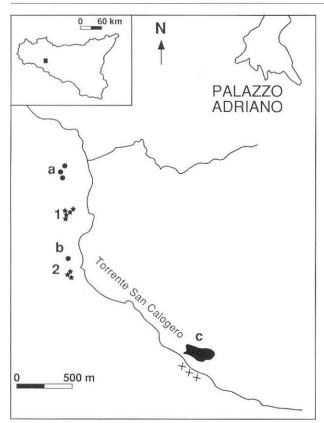


Fig. 4 Location of the investigated outcrops in western Sicily, Italy, Legend: Black) Predominantly Wordian Sosio Limestone klippes (slope facies with fusulinid-bearing shallow-water limestone blocks); a) Rupe di San Calogero and Pietra dei Saracini, three adjacent isolated limestone blocks, no longer accessible; b) Rupe del Passo di Burgio; Pietra di Salomone; Stars) Permian base of slope facies and Triassic cover; 1) Several outcrops ca. 350 m south of Pietra dei Saracini covering the Roadian (lowermost Middle Permian, Guadalupian Series) to Julian (middle Carnian) interval; 2) outcrops ca. 100 m SSW of Rupe del Passo di Burgio. Mainly lower Cathedralian (Cis-Uralian, Early Permian) turbidites well exposed west of a small road, along the road lower Cathedralian turbidites (partly exposed) and tectonically adjacent Changxingian red marls and thick calcarenites, no longer exposed, but small floated blocks of calcarenites still present. Crosses) Torrente San Calogero section, Permian deep basin facies and parts of the Triassic cover.

Occurrence: I. isarcica Zone of the type locality.

Remarks: *Sweetohindeodus tridentatus* n.sp. has two denticles on the blade behind the cusp that are distinctly shorter then the cusp.

Sweetohindeodus tridentatus n.sp.

(Pl. V, Fig. 5)

Derivation of name: According to the presence of three denticles (including the cusp).

Holotype: The specimen figured on Pl. V, Fig. 5; rep.-no. Ko 121191/IX-1.

Locus typicus: Lower Triassic section 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily.

Stratum typicum: Sample Ko 12 C, lower microconglomeratic calcarenite of the upper bed of the 2 m Geologia Croatica 49/1

thick calciturbidites above the lowermost Triassic shales. *Isarcicella isarcica* Zone of Lower Scythian.

Material: 2 specimens.

Diagnosis: The cup is circular. The blade is very short and bears a large erect cusp and two distinctly shorter, but also large, separated denticles.

Description: The cup is large, circular and its lower side is deeply excavated. The short blade bears on its free anterior part a large, erect, slender cusp. On the cup, the blade bears two large, separated denticles that are distinctly shorter than the cusp. The posterior one is slightly inclined backward. Its base is as broad as the base of the cusp. All denticles are slightly striated.

Occurrence: *I. isarcica* Zone of the type locality and of South China.

Remarks: This species is a transitional form to *Hindeodus*, in which the blade is longer and bears even in juvenile forms at least four denticles. The cup of *Hindeodus* is lanceolate or oval. *Sweetohindeodus bidentatus* n.sp. has only one very large denticle on the blade above the cup that is as long as the cusp.

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PLATE I

- 1-3, 5, 6 *Hindeodus typicalis* (SWEET), Pa element, x100, *Araxilevis* Beds (lowermost Dzhulfian = middle Wuchi-apingian), *Clarkina leveni* Zone, Achura (Azerbaidzhan); for sample locations see KOZUR et al. (1978, Fig. 1); Figs. 1, 3: sample 10/4, rep.-no. PK 1-5; Fig. 2: sample 10/3, rep.-no. PK 1-8; Figs. 5, 6: sample 10/2-2, rep.-no. PK 1-15.
- 4 *Hindeodus typicalis* (SWEET), Pa element, x100, sample AC 6 (see KOZUR et al., 1975), lower Dzhulfian (middle Wuchiapingian), Kuh-e-Ali Bashi at Julfa, northwest Iran, rep.-no. Ko 5740.
- 7 *Hindeodus typicalis* (SWEET), Sb element, x95, sample 10/3, *Araxilevis* Beds (lowermost Dzhulfian = middle Wuchiapingian), *Clarkina leveni* Zone, Achura (Azerbaidzhan), rep.-no. PK 1-5.
- 8 *Hindeodus typicalis* (SWEET), M element, x95, sample 10/3, *Araxilevis* Beds (lowermost Dzhulfian = middle Wuchiapingian), *Clarkina leveni* Zone, Achura (Azerbaidzhan), rep.-no. PK 1-8.
- 9 *Hindeodus julfensis* (SWEET), Pa element, advanced form with only 4 free denticles between the cusp and the smooth hump, x210, sample AR 35 (see KOZUR et al., 1975), lower Dorashamian (lower Changxingian), Kuh-e-Ali Bashi, northwest Iran, rep.-no. KMR 1975 I-1.
- 10 *Hindeodus latidentatus praeparvus* n.subsp., Pa element, specimen very similar to the *H. latidentatus latidentatus* (KOZUR, MOSTER & RAHIMI-YAZD), transitional form to this subspecies, x150, Tesero Oolite, 2 m above the Bellerophon Limestone, horizon with Changxingian brachiopods, upper Changxingian, Tesero (Southern Alps, Italy), rep-no. Ko 8992.
- 11 *Hindeodus latidentatus praeparuvus* n.subsp., Sb element, x160, Tesero Oolite, 2 m above the Bellerophon Limestone, horizon with Changxingian brachiopods, upper Changxingian, Tesero (Southern Alps, Italy), rep.-no. Ko 9208.

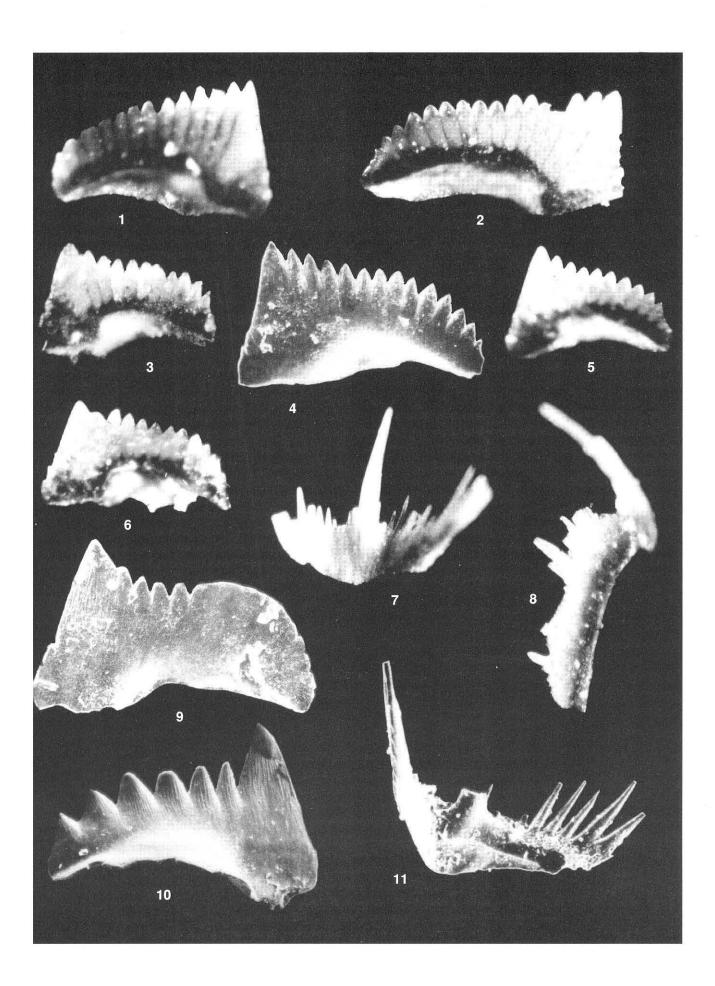


PLATE II

- 1-3 Hindeodus latidentatus praeparvus n.subsp., Pa element, Tesero Oolite, upper Changxingian, Tesero (Southern Alps, Italy); Fig. 1: x200, 2 m above the Bellerophon Limestone, horizon with Changxingian brachiopods, rep.-no. Ko 8991; Fig. 2: holotype, x180, 1.5 m above the Bellerophon Limestone, rep.-no. Ko 9003; Fig. 3: x200, 1.9 m above the Bellerophon Limestone, rep.-no Ko 8986.
- 4 *Hindeodus latidentatus praeparvus* n.subsp., Pa element, x220, Tesero Oolite, upper Changxingian, 0.3 m above the Bellerophon Limestone, Sass de Putia section (Southern Alps, Italy), rep.-no. Ko 8992 A.
- 5 *Hindeodus parvus* (KOZUR & PJATAKOVA), Pa element, slightly oblique later-lower view, primitive form, x160, upper Boundary Bed 2, Meishan section, re-figured from ZHANG (1987).
- 6 *Hindeodus parvus erectus* n.subsp., Pa element, holotype, the same specimen as in WANG (1994, Pl. 1, Fig. 1); x120, Zhongxin Dadui quarry of Meishan section, sample 882-4, upper part of Boundary Bed 2 (12-16 cm above its base), *H. parvus* Zone of lowermost Triassic, rep.-no. 123254.
- 7 *Hindeodus parvus parvus* (KOZUR & PJATAKOVA), Pa element, x95, sample 10/13 a-2 (see KOZUR et al., 1978), *I. isarcica* Zone, Achura (Azerbaidzhan), rep.-no. PK 1-7.
- 8 *Hindeodus parvus erectus* n.subsp., Pa element, x95, sample 10/13a-1 below the lower stromatolite horizon, *H. parvus* Zone, Achura (Azerbaidhan), rep.-no PK 1-4.
- 9,10 *Hindeodus postparvus* KOZUR, Pa element, x95, sample 10/13 a-2 (see KOZUR et al., 1978), *I. isarcica* Zone, Achura (Azerbaidzhan), rep.-no. PK 1-7.

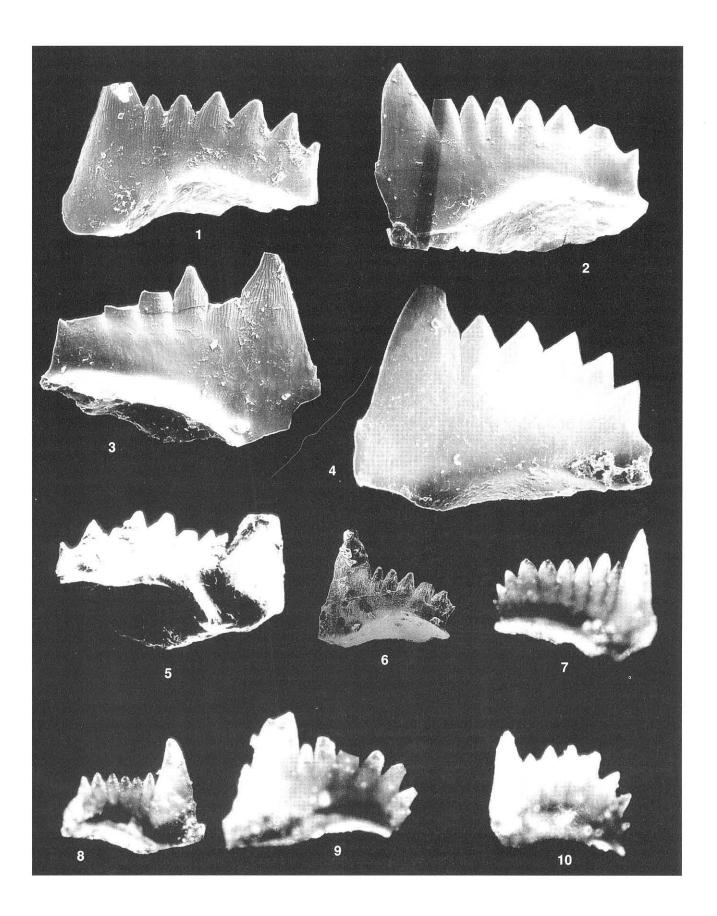


PLATE III

- 1-3, 5-10 Hindeodus parvus erectus n.subsp. from a monospecific fauna of predominantly juvenile specimens, sample Ko 14 (thin laminated limestone intercalation in 2 m thick yellowish-brown weathered, laminated, originally pyritic claystone at the base of the Triassic), *H. parvus* Zone. Section east of the road, 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (Italy), rep.-no. Ko 1994/I-1 (if not otherwise indicated); Figs. 1-3: Pa element of juvenile specimens, Fig. 1: x230, Fig. 2: x200, Fig. 3: x200, rep.-no. 16-8-95/I-18; Fig. 5: M element, x170; Fig. 6: Sb element, cusp and anteriormost denticle of the posterior bar on the strongly inward bent part of the unit, x140; Fig. 7: Pb element, x210; Fig. 8: Sc element, x130; Fig. 9: Pa element of adult specimen, x200, rep.-no. 16-8-95/I-10, a) lateral view, b) upper view; Fig. 10: Sb element, cusp on the strongly inward bent part of the unit, x200, rep.-no. 16-8-95/I-17.
- 4 *Hindeodus parvus erectus* n.subsp., Sa element, x200, sample Ko 12 a, uppermost part of graded calcarenites of Unit 2 (sensu GULLO & KOZUR, 1993), *I. isarcica* Zone, Lower Triassic section 350 m south of Pietra dei Saracini (Sosio Valley, Sicily), rep.-no. KoMo 14-4-94/V-34.
- Hindeodus cf. parvus erectus n.subsp., Pa element, specimen with unusually broad, distally rounded denticles, x200, sample KS 3 (floated block), lowermost Triassic graded calcarenite, east of the road 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (Italy), rep.-no. K 1994/I-2, a) lateral view, b) upper view.

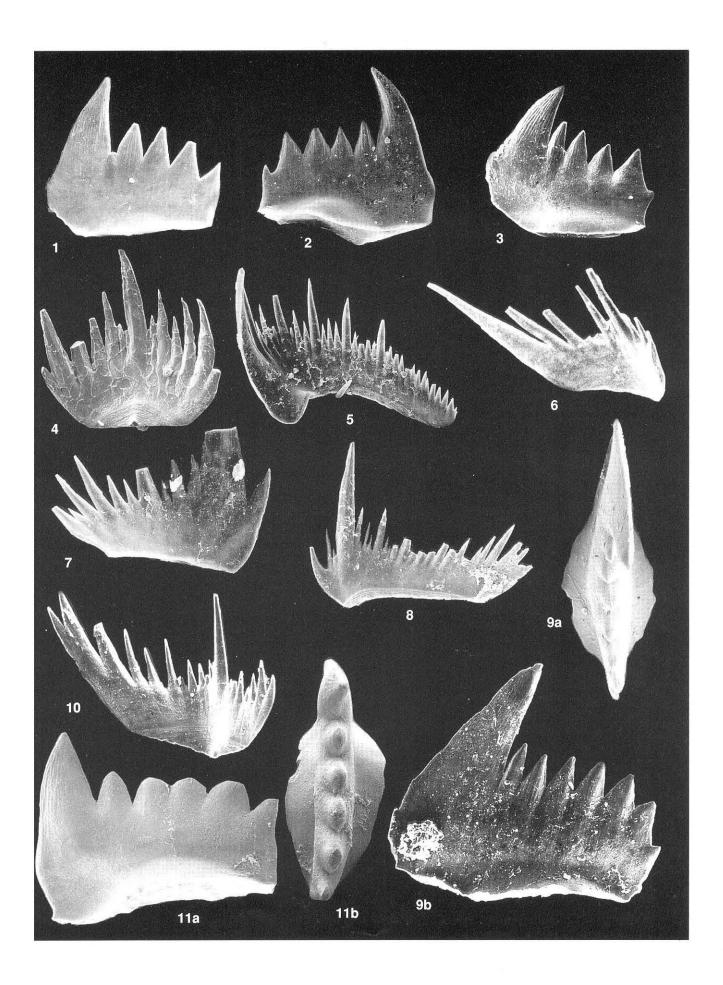


PLATE IV

- 1 *Hindeodus* cf. *typicalis* (SWEET), Pa element, slender cusp and a part of the denticles are broken and regenerated, therefore their original length may be larger, x95, sample KS 3 (floated block), lowermost Triassic graded calcarenite, east of the road 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (Italy), rep.-no. 4-12-94/VI-19.
- 2-4 *Hindeodus sosioensis* n.sp., x100, sample KS 3 (see Fig. 1); Fig. 2: Pa element, holotype, rep.-no. 4-12-94/VI-14; Fig. 3: Pb element, rep.-no. 4-12-94/VI-17; Fig. 4: Sb element, rep.-no. 4-12-94/VI-15.
- 5 Hindeodus parvus anterodentatus (DAI, TIAN & ZHANG), Pa element, primitive specimen, transitional to *H. parvus erectus*, x150, sample Ko 12 a, uppermost part of graded calcarenites of Unit 2 (sensu GUL-LO & KOZUR, 1993), *I. isarcica* Zone, Lower Triassic section 350 m south of Pietra dei Saracini (Sosio Valley, Sicily), rep.-no. KoMo 12-11-91/V-2.
- 6 *Hindeodus parvus erectus* n.subsp., Pa element, specimen with very high blade to demonstrate the large intraspecific variability, x150, sample KS 4 (floated block), lowermost Triassic graded calcarenite, east of the road 350 m south of Pietra dei Saracini, Sosio Valley, western Sicily (Italy), rep.-no. 4-12-94/VI-22.
- 7 *Hindeodus parvus erectus* n.subsp., Pa element with distally rounded denticles, x200, sample KS 3 (see Fig. 1), rep.-no. Ko 1994/I-3, a) lateral view, b) upper view, cup not thickened.
- 8 *Isarcicella? turgida* (KOZUR, MOSTLER & RAHIMI-YAZD), Pa element, primitive form, thickened and unthickened part of the cup nearly of the same width, x200, sample KS 3 (see Fig. 1), rep.-no. Ko 1994/I-4, a) lateral view, b) upper view, thickened inner part of the cup well recognizable.
- 9 *Isarcicella? prisca* n.sp., Pa element, holotype, re-figured from PERRI (1991, Pl. 3, fig. 1), x95, sample Bu 10, lower Tesero Oolite, upper Changxingian, Bulla section, SW of Ortisei (Southern Alps, Italy), locality and sample data see PERRI, 1991, rep.-no. IC 1444, a) lower view, b) upper view, c) lateral view.

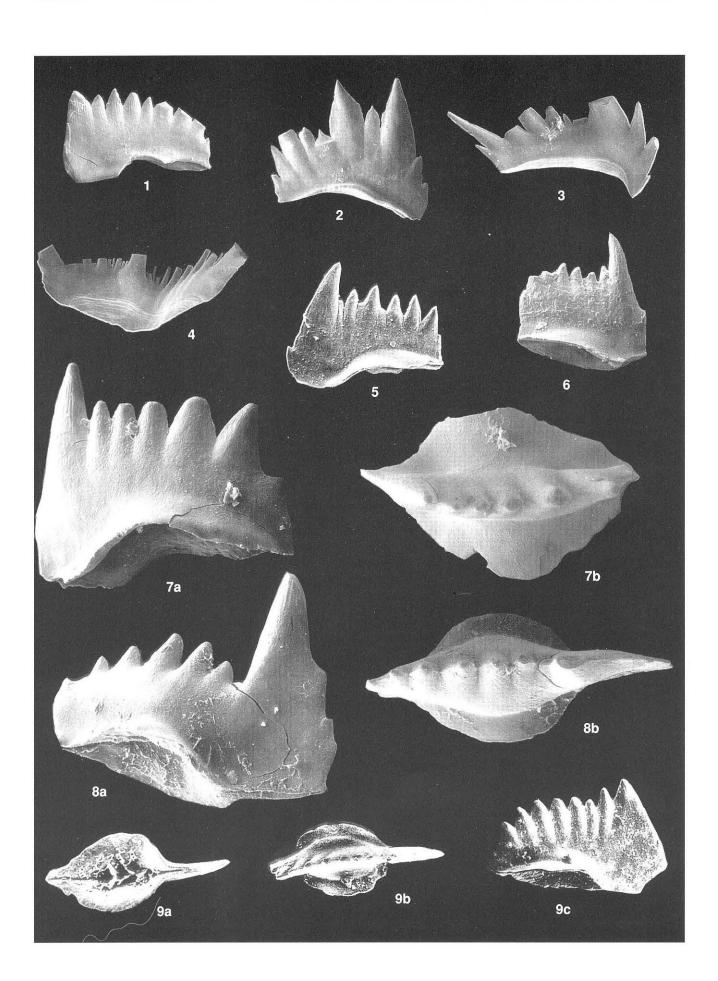


PLATE V

Hindeodus changxingensis WANG, Pa element, x 80, sample 882-1, lower 4 cm of Bed 27 (Boundary Bed 2), uppermost Changxingian, Zhongxin Dadui quarry of Meishan section, South China (see Figs. 1, 2), rep.-no. AEL-882-1/123246.

- 2 *Hindeodus changxingensis* WANG, Pa element, specimen figured by WANG (1994, Pl. 1, Fig. 11) and WANG (1995 b, Pl. 3, Fig. 1) as *Hindeodus julfensis* (SWEET), x82, sample 882-3, at 8-12 cm above the base of Bed 27 (Boundary Bed 2), lowermost Triassic, lower *H. parvus* Zone, Zhongxin Dadui quarry of Meishan section, South China (see Figs. 1, 2), rep.-no. AEL-882-3/123247.
- 3 *Sweetohindeodus bidentatus* n.gen. n.sp., Pa element, lateral view, x280, sample Ko 12 a, uppermost part of graded calcarenites of Unit 2 (sensu GULLO & KOZUR, 1993), *I. isarcica* Zone, Lower Triassic section 350 m south of Pietra dei Saracini (Sosio Valley, Sicily), rep.-no. 121191/IX-3.
- 4 *Sweetohindeodus bidentatus* n.gen. n.sp., Pa element, holotype, sample Ko 12 a (see fig. 3), rep.-no. 12-11-91/IX-2, a) upper view, x260, b) lateral view, x170.

5 *Sweetohindeodus tridentatus* n.sp., Pa element, holotype, sample Ko 12 c, upper bed of the graded limestone (Unit 2 by GULLO & KOZUR, 1993), *I. isarcica* Zone, locality as for fig. 3, rep.-no. 12-11-91/IX-1, a) upper view, x200, b) lateral view, x150.

- 6 *Isarcicella isarcica staeschei* (DAI & ZHANG), x150, sample 21.4, *I. isarcica* Zone, Dorasham II (for sample data see KOZUR et al., 1978), rep.-no. Ko 1465, a) lateral view, b) oblique lateral view to show the transition of the thickened inner part of the cup to the unthickened marginal part of the cup, c) upper view.
- 7,8 Isarcicella? turgida (KOZUR, MOSTLER & RAHIMI-YAZD), Pa element; Fig. 7: lateral view, x120, sample 2092, Unit 2 sensu GULLO & KOZUR (1993), middle part of the upper bed of the 2 m thick lower calcarenite horizon, lower *I. isarcica* Zone, lower Brahmanian ("Induan"), section 350 m south of Pietra dei Saracini, Sosio Valley area, Sicily, rep.-no. G 91/IX-15; Fig. 8: upper view of an other specimen, x80, sample Ko 12 B, age and locality as for Fig. 7, rep.-no. 12-11-91/IX-4.
- 9 *Isarcicella isarcica isarcica* (HUCKRIEDE), Pa element, lateral view, x150, sample 21.4 (see Fig. 6), rep.-no. Ko 1467.
- 10, 11 Hyphae of marine fungi (Ascomycetes), probably of *Tympanicysta stoschiana* BALME, upper Changxingian Tesero Oolite, 0.30 m above the Bellerophon Limestone, Sass di Putia section (Southern Alps, Italy); Fig. 10: x110, rep.-no. Ko 8984; Fig. 11: isolated hypha, x200, rep.-no. Ko 8975.

