THE LOWER TRIASSIC (SCYTHIAN) AMMONOID *OTOCERAS*

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Abstract. The ammonoid genus *Otoceras* has long been recognized as identifying the lowest Triassic (Scythian) zone. The genus was first described from the Himalayas and is now known from Siberia and from Arctic North America. Diener (1897) recognized seven species of *Otoceras* in his collections from the Himalayas; data are presented to demonstrate that only one species—*O. woodwardi* Griesbach—is present. In addition the circum-Arctic *Otoceras boreale* Spath and *O. indigirense* Popov are considered to be subspecies of *O. woodwardi* Griesbach. Associated with *Otoceras* in the Himalayas is the genus *Ophiceras*, which is by far the predominant element in the fauna. Wherever it occurs *Otoceras* tends to be quite rare. A number of other genera have been reported from the *Otoceras-Ophiceras* Zone, and each of these is reviewed in detail. Analysis of the worldwide extent of this zone suggests that *Otoceras* did not survive as long in the Arctic as it did in Tethys.

Otoceras is a direct descendant of the late Permian genus *Pseudotoceras* of the family Araxoceratidae Ruzhentsev and is the last surviving element of that evolutionary lineage. The family Otoceratidae Hyatt (1900) should take precedence over the name Araxoceratidae Ruzhentsev (1959).

INTRODUCTION

The first proposed sequence of zones for the marine Triassic of "pelagic facies," by Mojsisovics, Waagen, and Diener (1895), listed as the basal Triassic zone that of *Otoceras woodwardi*, a species first described by Griesbach (1880) from the Himalayas and thoroughly monographed by Diener (1897). Ever since that time *Otoceras* has been recognized as a primary index fossil of the lowest Triassic zone. At the same time it was recognized that the associated genus *Ophiceras* also was a marker of the lowest Triassic. It has been a matter of complete orthodoxy that *Otoceras* identifies the lowest zone of the Triassic. It has also been taken as a matter of course that *Otoceras* was a descendent of so-called primitive "otocerids" first recorded by Abich (1878) from the Upper Permian of Soviet Dzhulfa. One of the most interesting discoveries of the last decade has been the recognition of a large-scale and significant radiation of the so-called "otocerids" in the late Permian (Ruzhentsev, 1959, 1962, 1963). This radiation is expressed by nine genera and 30 species from the Dzhulfian strata of Soviet Dzhulfa representing an extremely complex array of forms, brought together in the family Araxoceratidae by Ruzhentsev (1959). Among the genera of this family is one genus, *Pseudotoceras*, that appears to be the direct ancestor of *Otoceras*. The data available lead to the conclusion that *Otoceras* is the final evolutionary descendant of the late Permian radiation of the "otocerids."

The primary purpose of this contribution is to review the evolutionary and biostratigraphic status of the genus *Otoceras*. Soon after the introduction of the genus and its type species by Griesbach (1880), a number of new species were introduced by Diener (1897). The thesis presented here is that only one species of the genus is present in the lowest Triassic beds of the

Himalayas. In addition it is proposed that *Otoceras boreale* Spath of northern Alaska, Arctic Islands of Canada, Spitsbergen, and northwestern Siberia is a subspecies of the Tethyan *Otoceras woodwardi.* Another conclusion of this review is that the family Araxoceratidae Ruzhentsev is, from an evolutionary viewpoint, best placed in synonymy of the older family Otoceratidae Hyatt (1900).

Finally it is suggested that *Otoceras woodwardi* survived in the earliest Triassic in the circum-Arctic region for a shorter period of time than in Tethys.

ACKNOWLEDGMENTS

In June of 1970 I had the opportunity of visiting the Paleontological Institute in Moscow and the Geological Institute in Leningrad to discuss with Soviet specialists the Permian-Triassic boundary beds of Soviet Dzhulfa. One result of these discussions was a need for a thorough review of the genus *Otoceras* and the lowest Triassic (Scythian) zone, and this paper is an attempt to serve that goal. I have been most fortunate in the reading and comments on the manuscript by W. M. Furnish, B. F. Glenister, N. D. Newell, Norman F. Sohl, and Curt Teichert. Miss Victoria Kohler ably assisted throughout preparation of the manuscript, especially in preparation of the plates and text-figures. Mrs. Agnes Pilot cheerfully typed the various drafts of the manuscript. Study of the type collections of ammonoids from the *Otoceras-Ophiceras* Zone of the Himalayas deposited in the Geological Survey of India in Calcutta was made possible by N.S.F. grant G-19066. Further work on these faunas was supported by N.S.F. grant GB-12909. My visit to the Soviet Union was supported by a grant from the Shaler Fund of Harvard University.

Otoceras—Morphology and Intraspecific Variation

All workers on the Himalayan ammonite genus *Otoceras* (Griesbach, 1880; Diener, 1897; v. Krafft and Diener, 1909; and Spath, 1930, 1934, 1935) are agreed as to the great variability in most if not all of its shell characters. Disagreement exists, though, in the taxonomic treatment of the genus. Griesbach concluded that "though it seems that there are several varieties, if not species, amongst the numerous specimens obtained, I prefer to include them for the present under one collective name" (Griesbach, 1880: 106). Diener (1897: 154) concurred with Griesbach's suspicion that "several varieties if not species" were represented, but at the same time added that "the distinction of the different species, or rather, the selection from among the numerous forms, which are all alike and all again different from each other, of those which ought to be considered as proper species, is no easy matter. For in no genus of Triassic ammonites known to

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Figure 1. Diagrammatic representation of the suture of specimens of *Octoceras woodwardi woodwardi* Griesbach from *Otoceras* beds in the Himalayas. A, topotype *O. woodwardi* (Diener, 1897, pl. 2, fig. 1; Pl. 2, figs. 3, 4 of this report) at a whorl height of approximately 45 mm, GSI 5924; B, topotype *O. woodwardi* (Diener, 1897, pl. 5, fig. 3; Pl. 1, figs. 5, 6 of this report) at a whorl height of 35 mm, GSI 5937; C, topotype *O. woodwardi* (Diener, 1897, pl. 5, fig. 5; Pl. 1, figs. 9, 10 of this report) at a whorl height of 27 mm, GSI 5939; D, paralectotype *O. woodwardi* (Diener, 1897, pl. 4, fig. 4; Pl. 1, figs. 3, 4 of this report) at a whorl height of 27 mm, GSI 5932; E, topotype *O. woodwardi* (Frech, 1902: 575, fig. 4d) at a whorl height of 21 mm; F, topotype *O. woodwardi* (Diener, 1897, pl. 4, fig. 5; Pl. 1, figs. 11, 12 of this report) at a whorl height of 13 mm, GSI 5933; G, topotype *O. woodwardi* (Frech, 1902: 575, fig. 4e) at a whorl height of 11 mm; H, topotype *O. woodwardi*, at a whorl height of 3.2 mm, BM(NH) C28513; I, holotype *O. undatum* (Diener, 1897, pl. 4, fig. 6; Pl. 3, figs. 9, 10 of this report) at a whorl height of approximately 20 mm, GSI 5934; J, holotype *O. parbati* (Diener, 1897, pl. 4, fig. 1; Pl. 4, figs. 9, 10 of this report) at a whorl height of 30 mm, GSI 5929; K, syntype *O. clivei* (Diener, 1897, pl. 5, fig. 4; Pl. 3, figs. 5, 6 of this report) at a whorl height of approximately 32 mm, GSI 5938; L, syntype *O. clivei* (Diener, 1897, pl. 3, fig. 4; Pl. 3, figs. 1, 2 of this report) at a whorl height of 35 mm, GSI 5928; M, suture specimens *O. clivei* (Diener, 1897, pl. 7, fig. 17; Pl. 3,

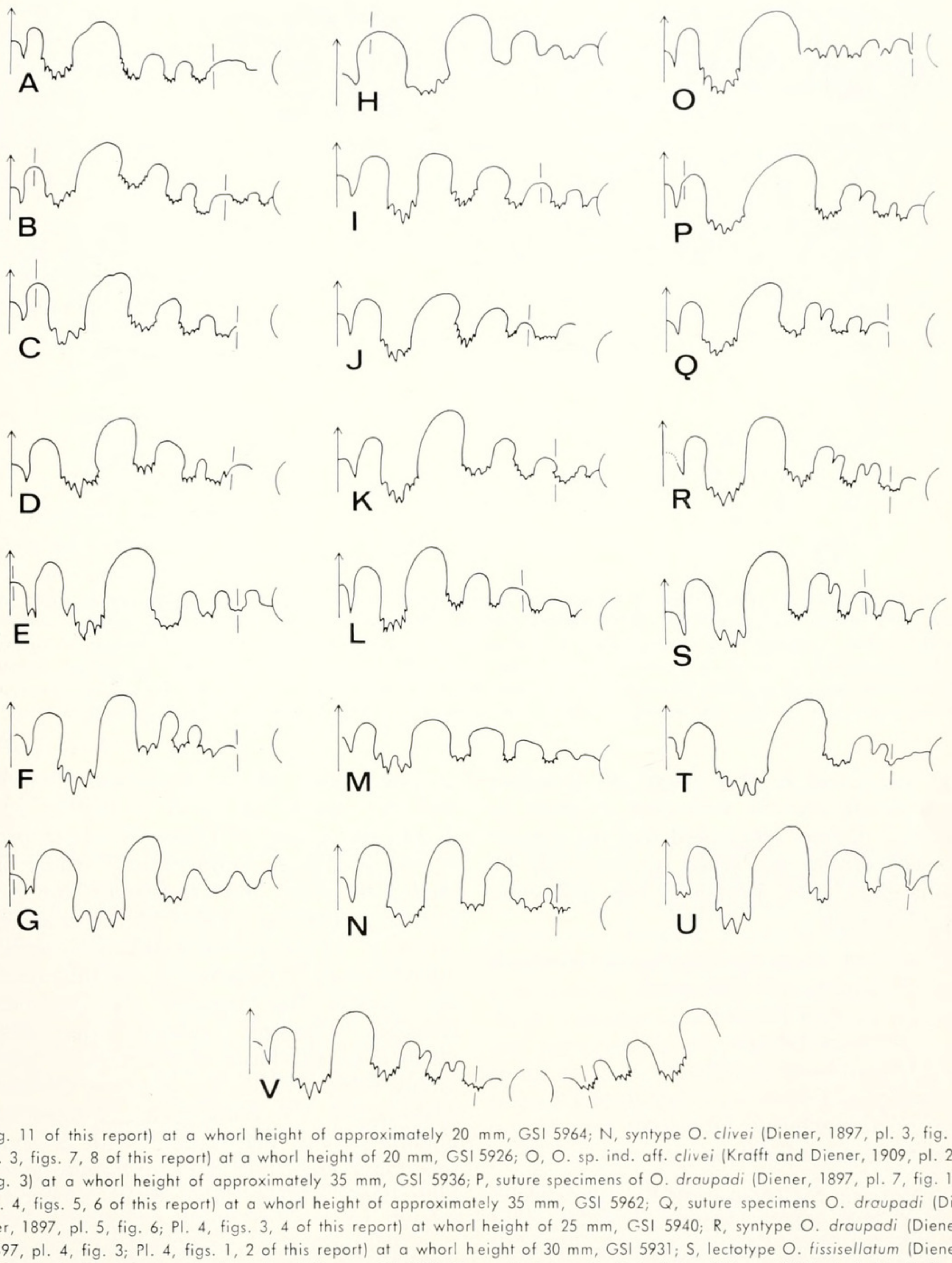

fig. 11 of this report) at a whorl height of approximately 20 mm, GSI 5964; N, syntype *O. clivei* (Diener, 1897, pl. 3, fig. 2; Pl. 3, figs. 7, 8 of this report) at a whorl height of 20 mm, GSI 5926; O, *O.* sp. ind. aff. *clivei* (Krafft and Diener, 1909, pl. 29, fig. 3) at a whorl height of approximately 35 mm, GSI 5936; P, suture specimens of *O. draupadi* (Diener, 1897, pl. 7, fig. 15; Pl. 4, figs. 5, 6 of this report) at a whorl height of approximately 35 mm, GSI 5962; Q, suture specimens *O. draupadi* (Diener, 1897, pl. 5, fig. 6; Pl. 4, figs. 3, 4 of this report) at whorl height of 25 mm, GSI 5940; R, syntype *O. draupadi* (Diener, 1897, pl. 4, fig. 3; Pl. 4, figs. 1, 2 of this report) at a whorl height of 30 mm, GSI 5931; S, lectotype *O. fissisellatum* (Diener, 1897, pl. 3, fig. 3c) at a whorl height of 25 mm, GSI 5927; T, paralectotype *O. fissisellatum* (Diener, 1897, pl. 5, fig. 2; Pl. 4, figs. 7, 8 of this report) at a whorl height of 25 mm, GSI 5936; U, *O.* (*Metotoceras*) *dieneri* Spath = *Hungarites* sp. indet. (Diener, 1897, pl. 23, fig. 5; Pl. 3, figs. 3, 4 of this report) at a whorl height of 27 mm, GSI 6058; V, left and right suture of syntype of *O. draupadi* (Diener, 1897, pl. 4, fig. 3; Pl. 4, figs. 1, 2 of this report) at a whorl height of approximately 25 mm, GSI 5931.

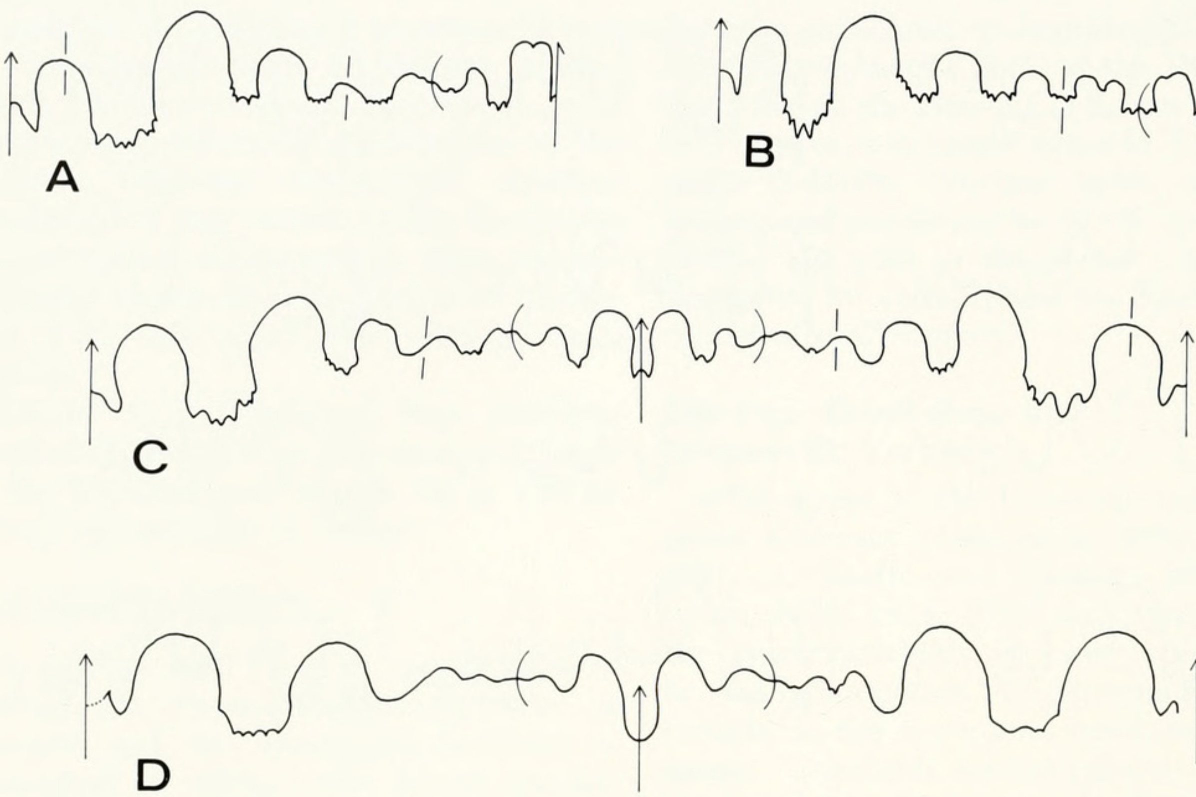

Figure 2. Diagrammatic representation of the sutures of specimens of *Otoceras woodwardi woodwardi* Griesbach from *Otoceras* beds, Shalshal Cliff near Rimkin Paiar encamping ground, Niti region, Himalayas. A, complete suture of specimen figured on Plate 2, figures 5–7 at a whorl height of 11.8 mm, BM(NH) 28512; B, complete suture of specimen of *Otoceras clivei* (Diener, 1897, pl. 7, fig. 16; illustrated here on Plate 3, figure 12) at a whorl height of 25 mm, GSI 5963; C, complete left and right suture of specimen figured on Plate 2, figures 8–10, at a whorl height of 5.7 mm, BM(NH) C28514; D, complete left and right suture of specimen figured on Plate 2, figures 13–15, at a whorl height of 1.5 mm, BM(NH) C28513b.

me, not even in the group of *Dinarites spiniplicati,* are the variations so great as in this." Diener concluded that the sutures showed criteria by which species could be recognized, and proposed the following classification:

Group of *Otoceras woodwardi* Griesbach
- *O. woodwardi* Griesbach
- *O. parbati* Diener
- *O. clivei* Diener
- *O. undatum* Griesbach

Group of *Otoceras fissisellatum* Diener
- *O. fissisellatum* Diener
- *O. draupadi* Diener

The basis for separating the two species groups was the presence or absence of small secondary lobes in one or more of the lateral saddles. The group of *Otoceras fissisellatum* has such secondary lobes, whereas the species of the group of *O. woodwardi* do not have them. The place of intersection of the umbilical shoulder and the suture was used to further subdivide the group of *Otoceras woodwardi.* In one of these subdivisions, which includes *O. clivei* and *O. parbati,* the first auxiliary saddle is divided by the umbilical shoulder. In the second subdivision, which includes only *O. woodwardi,* the first auxiliary saddle lies outside the umbilical shoulder. *Otoceras undatum* was distinguished on the basis of presence of wavy, lateral folds. Within the group of *Otoceras fissisellatum* the name-giving species has generally only one saddle with a small secondary lobe, but in *O. draupadi* generally two saddles have small secondary lobes.

That the suture of the Himalayan *Otoceras* was highly variable was freely admitted by Diener (1897). Griesbach (1880: 107) was the first to note that in some of his specimens the sutures varied in details

TABLE 1. TABULATION OF SPECIMENS PER LOCALITY FROM *OTOCERAS-OPHICERAS* BEDS IN THE HIMALAYAS AVAILABLE TO DIENER (1897).
Locality of specimens studied by von Krafft and Diener (1909) indicated by an X. These authors generally did not indicate the precise number of specimens in their collections but it appears to have been very few for each species.

	Muth	Ensa	Kuling	Kaga	Tengdi	Khar	Gaichund	Kiunglung	Shalshal
Episageceras dalailamae	X			X					2
Ophiceras sakuntala	X	X		X				6	140
medium								5	5
tibeticum	X	X	X	X		3		16	13
gibbosum									10
demissum					5	X		11	12
ptychodes									3
chamunda			2			2	X	3	30
platyspira								1	6
serpentinum						2		37	1
Glyptophiceras himalayanus									1
Proptychites scheibleri									1
Vishnuites pralambha									2
Otoceras woodwardi	X	X	X			X		1	31
undatum		X							2
clivei	X	X	1				X		7
draupadi									5
parbati								1	
fissisellatum									4
Prionolobus hodgsoni									2
Anotoceras nala								5	1

of the elements on the left and right sides of the specimens. Diener (1897: 155) described and illustrated a suture in which "the specimen is a perfect *Otoceras woodwardi* on one, and a perfect *O. draupadi* on the other side." The sutures of the various species of *Otoceras* from the Himalayas reproduced by Diener (1897) are illustrated here in Figure 1. The sutures of three small specimens in the British Museum (Natural History) are shown in Figure 2. In two of these specimens the complete suture could be observed, and showed obvious minor differences on the two sides of the conch (Fig. 2C, D).

As I have shown (Kummel, 1969), sutures of many Scythian ammonoids exhibit the same high degree of variability as any other morphological feature.

Diener (1897) recorded that he had 56 specimens of *Otoceras* from the Shalshal Cliff locality, opposite the Rimkin Paiar encamping ground, most of which came from the so-called main layer of *Otoceras woodwardi*, a unit only one foot thick. Of these specimens only the 17 figured by him are preserved in the Geological Survey of India at Calcutta. Diener (1897: 154) observed that "the relative proportions of height and thickness and the size of the umbilicus are so variable, even in specimens which agree in all other characters, that they cannot serve for specific distinction." Considering the fact that all 56 specimens from Shalshal Cliff, which provided the main material for Diener's study, came from a one-foot thick bed at one locality it appears more logical to consider

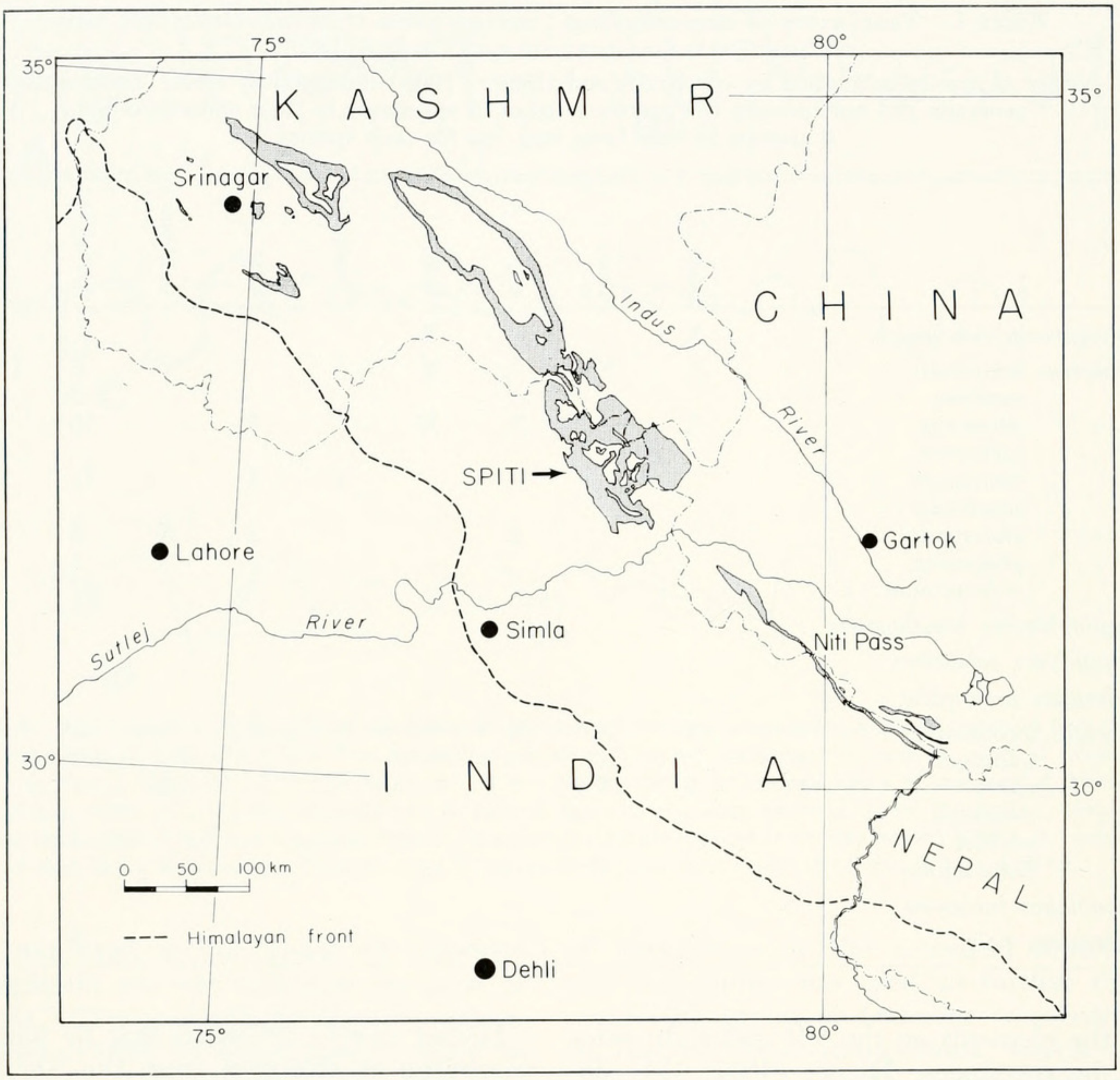

Figure 3. Outcrop map of Triassic formations in the Himalayas (from Geological Map of India, Geological Survey of India, 1957).

this assemblage as a natural population, in which variations in sutures are no more than what one would expect. On Table 1 are listed the numbers of specimens of each species of *Otoceras* Diener recognized in the Shalshal fauna. Of the 56 specimens of *Otoceras,* 31 were assigned to *O. woodwardi* and only four specimens to *O. fissisellatum,* which has a small lobe in the first auxiliary saddle; *O. draupadi,* which has a small lobe in each of the first and second auxiliary saddles, is represented by five specimens, and *O. clivei* by only seven specimens. The sutures of the specimens assigned to species other than *O. woodwardi* are no more than intraspecific variants. Although presence or absence of a minor lobe in an auxiliary saddle is conspicuous, it does not necessarily represent a specific difference. This suggestion could, of course, only be tested by examination of large population samples. The specimens of *Otoceras* recorded by von Krafft and Diener (1909) from Spiti are few in number and poorly preserved. All the localities that have yielded the *Otoceras-Ophiceras* fauna studied by Diener (1897) and von Krafft and Diener (1909)

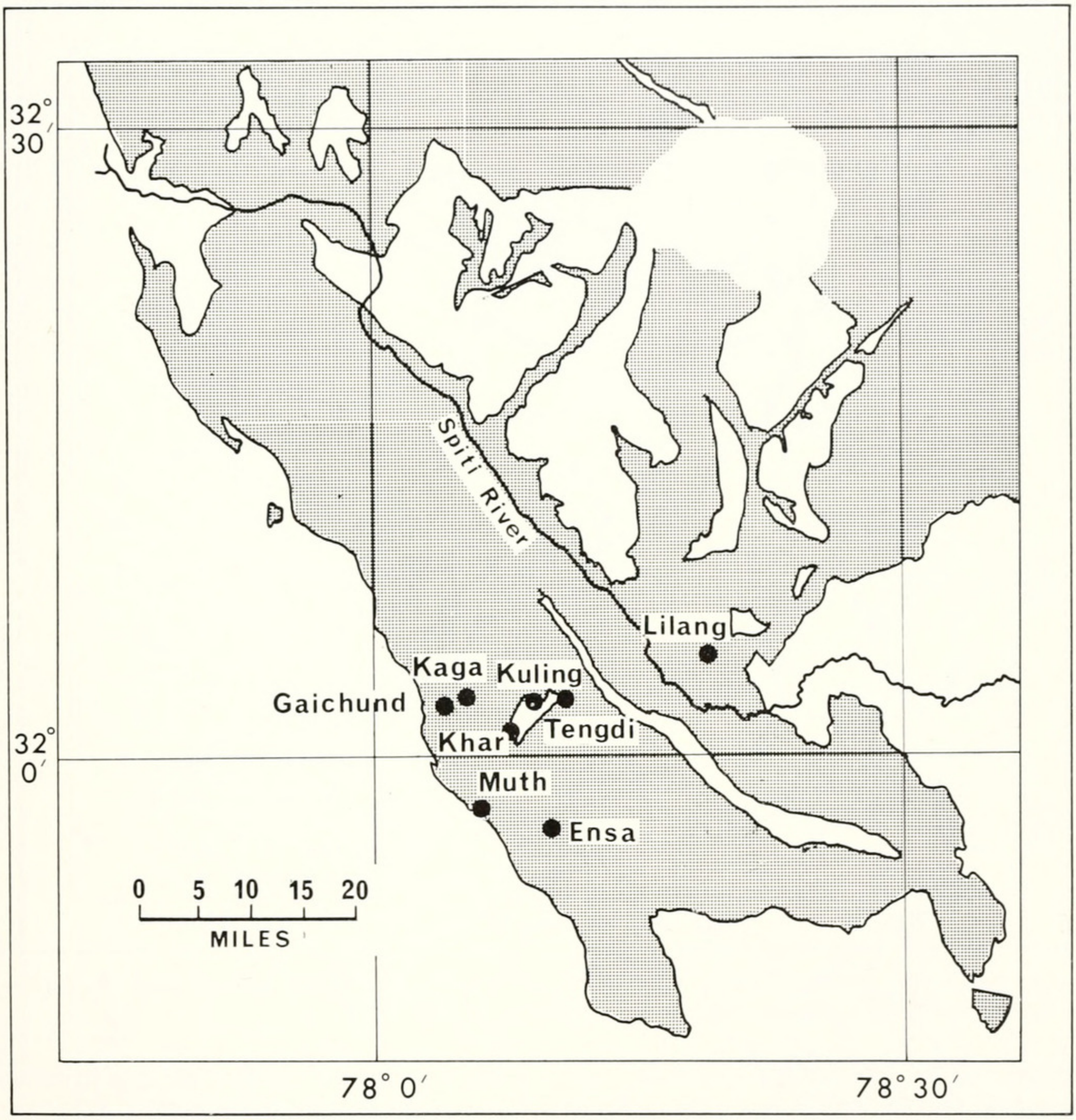

Figure 4. Outcrop map of Triassic formations in the Spiti region showing principal localities that have yielded faunas from the *Otoceras-Ophiceras* Zone (adapted from H. H. Hayden, 1904, pl. 18).

are shown on Figures 3 to 5. The Eigil Nielsen collection in Copenhagen from Muth in the Spiti region contains 14 specimens of *Otoceras*, all poorly preserved.

The descriptions of the Himalayan otocerids by Diener (1897) are quite thorough, and examination of his figured specimens leaves little to be added. As all of Diener's illustrations were line-drawings, unretouched photographs of the types are published here (Plates 1–4). It can readily be seen that Diener's drawings tended to be idealized and do not indicate the general state of preservation. The smallest specimen described by Diener is approximately 28 mm in diameter (Pl. 1, figs. 11, 12) and was assigned by him to *O. woodwardi*. The tray in the collections of the Geological Survey of India that contains Griesbach's lectotype (Pl. 1, figs. 1, 2) also

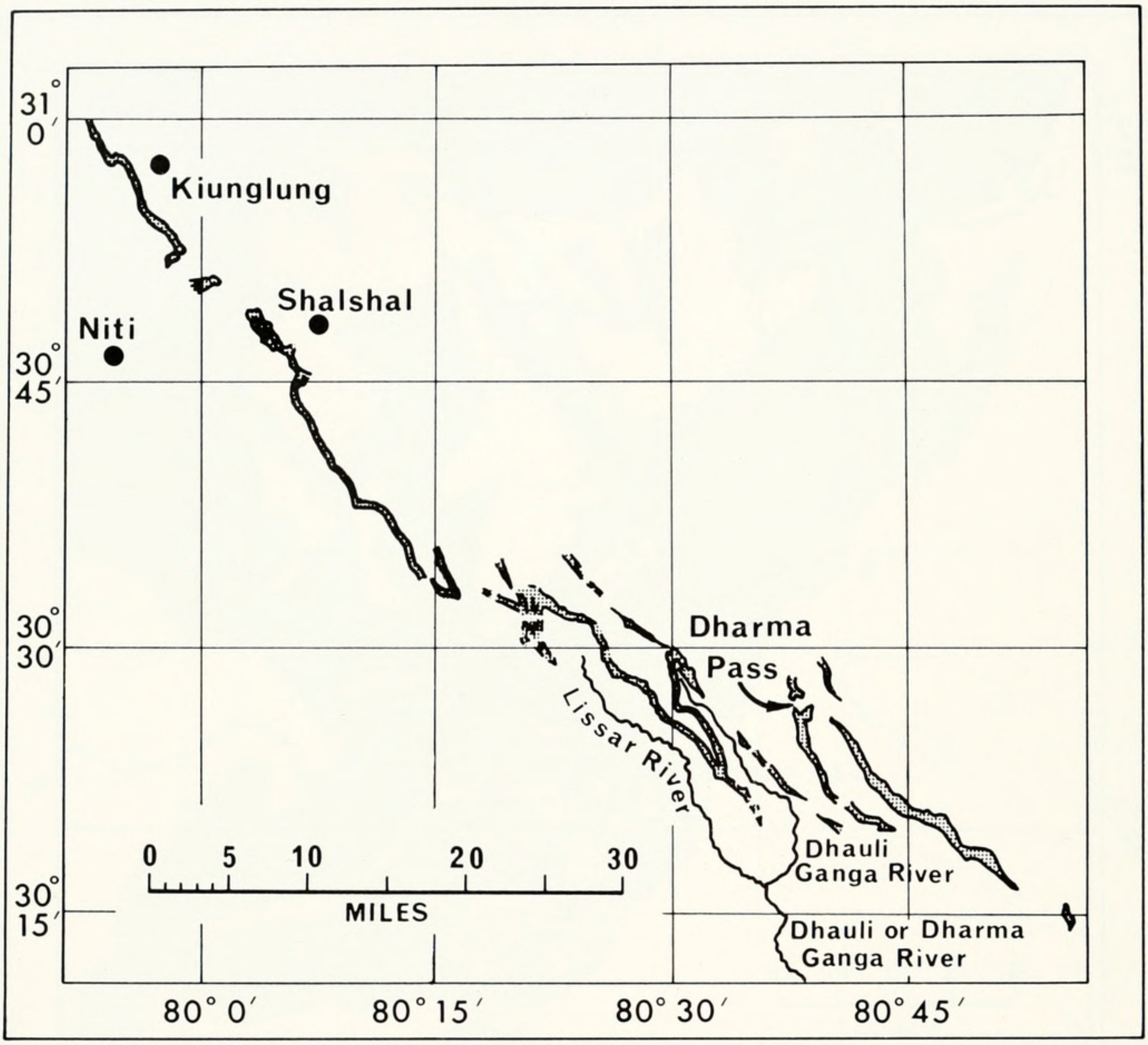

Figure 5. Outcrop map of Triassic formations in the Niti Pass region showing the principal localities that have yielded faunas from the *Otoceras-Ophiceras* Zone (adapted from C. L. Griesbach, 1891, Map No. 1).

contains an unnumbered specimen, not figured by Diener, which has a diameter of 9 mm (Pl. 1, figs. 7, 8). The collections of the British Museum (Natural History) contain some fragmentary specimens from the Shalshal Cliffs, including fragments of inner whorls. The smallest specimen is a third whorl section with a height of 1.8 mm (Pl. 2, figs. 13–15). At that whorl height the median keel is well marked, but the dorsal area shows no impression of a keel. The lateral keels adjoining the ventral keel are just faintly visible. The lateral areas bear two broad, low folds. The complete suture of this specimen is illustrated in Figure 2D. Another specimen, having a diameter of approximately 8.5 mm, shows the three ventral keels very well (Pl. 2, figs. 11, 12). A third specimen (Pl. 2, figs. 8–10) has a diameter of 13.5 mm. Its complete suture at a whorl height of 5.7 mm is reproduced in Figure 2C.

I include in *Otoceras woodwardi* of the Himalayas the specimen Diener (1897: 150) described as *Hungarites* sp. ind., here illustrated on Plate 3, figures 3, 4. Diener recognized the close similarity of this fragmentary specimen of a third volution to *Otoceras woodwardi.* He, however, considered it distinct because the "remarkable difference from *Otoceras* is in the denticulate development of the siphonal lobe,

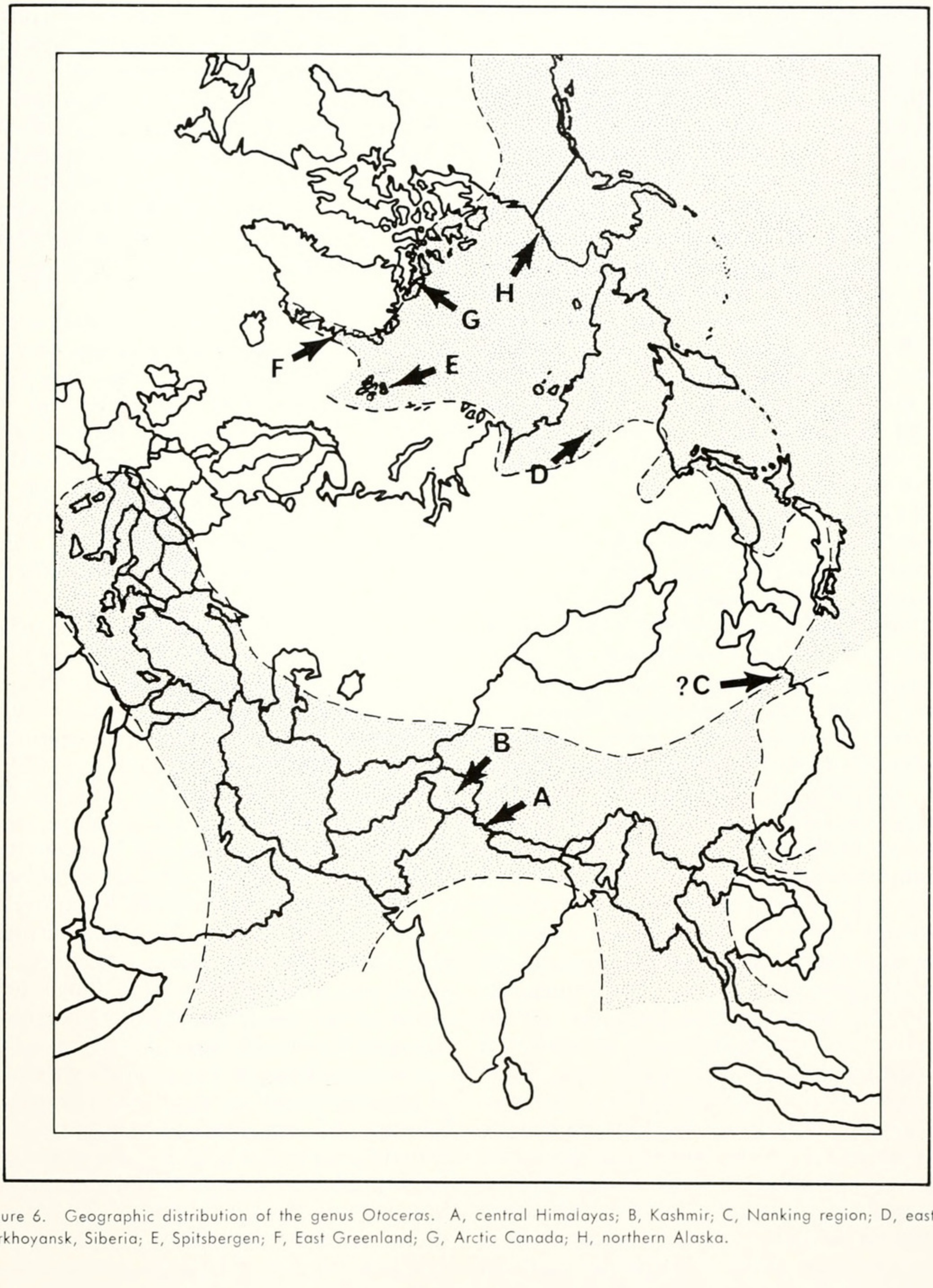

Figure 6. Geographic distribution of the genus *Otoceras*. A, central Himalayas; B, Kashmir; C, Nanking region; D, eastern Verkhoyansk, Siberia; E, Spitsbergen; F, East Greenland; G, Arctic Canada; H, northern Alaska.

which is bifid in *Otoceras*, whereas each of its lateral branches is denticulate in *Hungarites*" (Diener, 1897: 150). The ventral lobe, in fact, is trifid on one side and bifid on the other (Diener, 1897, pl. 23, fig. 5c; Fig. 1V of this report). The auxiliary series is not as fully developed as in the specimens assigned to *Otoceras* but, here again, the differences are not considered to be significant. All characters of this specimen fall well within the range of variability of *Otoceras woodwardi*. Spath (1930: 8) proposed the subgenus *Metotoceras* for Diener's specimen of *Hungarites* sp. ind., making special note of the absence of an umbilical rim; however, such a rim is present on the adoral portion of the specimen (Pl. 3, fig. 3).

Within Tethys *Otoceras* of earliest Scythian age is known only from the Himalayas, the Niti and Spiti regions of Kumaon, and in Kashmir near Srinagar. Recently Nakazawa et al. (1970) have illustrated several well-preserved specimens that they assign to *O. clivei* Diener and *O. draupadi* Diener from the Guryul Ravine, Kashmir. The other localities where the genus has been recorded are in the circum-arctic region (Fig. 6). The genus was first recorded from East Greenland by Spath (1930), who assigned a few fragmentary specimens to *Otoceras fissisellatum*. A larger collection was available to Spath (1935) in a later report where he introduced the name *Otoceras boreale* for the East Greenland forms. The genus *Otoceras* was next reported from the eastern Verkhoyansk region by Popov (1958), who recognized two species—*O. boreale* Spath and *O. indigirense* Popov. The latter species, which was based on four specimens, was separated on the basis of the presence of a vertical umbilical wall and slight differences in the sutures. In North America *Otoceras boreale* has been reported from the Canning River region of northern Alaska (Kummel *in* Reeside et al., 1957: 1501) and described and illustrated from Ellesmere and Axel Heiberg Islands (Tozer, 1961, 1967). The lowest Triassic fauna on Axel Heiberg Island has yielded a small number of specimens of a single species that Tozer (1967) described as *Otoceras concavum*, considering concave flanks on the inner whorls as distinguishing characters. Considering the range of variability seen in the larger Himalayan fauna, I find it difficult, on the basis of such a small sample, to recognize *O. concavum* as a distinct species.

The only author who attempted a general assessment of the relationships between the Arctic *O. boreale* and the species of *Otoceras* known from the Himalayas was Spath (1930, 1934, 1935). It was in his second report on the East Greenland Lower Triassic fauna that Spath, on the basis of much larger faunas, recognized *O. boreale* as being distinct from the Himalayan species of the genus, justifying his separation of these forms on the basis of slight differences in the suture, especially in the dorsal suture (Spath, 1935: 11). Information on the dorsal suture of *Otoceras woodwardi* is limited. Griesbach (1880, pl. 2, fig. 6) reproduced a complete suture of *O. woodwardi* and so did Diener (1897, pl. 7, fig. 16; Fig. 2B of this report). The specimen which yielded the suture reproduced by Diener is figured here on Plate 3, figure 12. Though there are differences in detail between the sutures illustrated by Griesbach and Diener, there is a suspicion that they were both taken from the same specimen. Frech (1901: 575) illustrated a series of sutures taken at whorl heights of 2.5 mm, 6 mm, 11 mm, and 21 mm. The complete sutures of three small specimens of *Otoceras woodwardi* at whorl heights of 1.5 mm, 5.7 mm, and 11.8 mm are illustrated in Figures 2A, C, D. There are only three published sutures of *Otoceras boreale* that include the dorsal suture, but two of these are incomplete (Fig. 7). In *Otoceras boreale* the dorsal lateral saddles contain adventitious lobes that are larger than in those of *O. woodwardi*. However, the three dorsal sutures of *O. boreale* were taken at

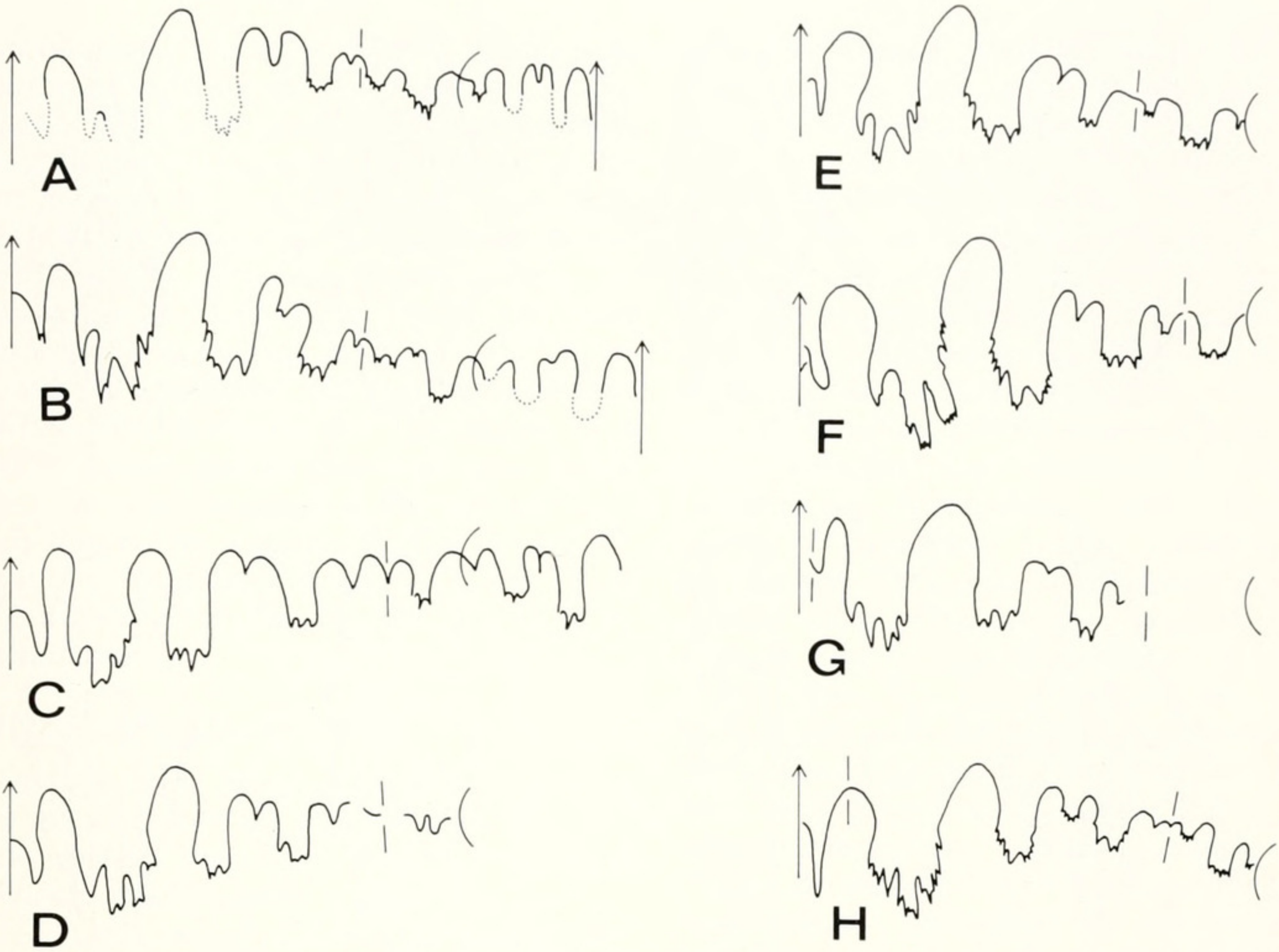

Figure 7. Diagrammatic representation of the suture of specimens of *Otoceras woodwardi boreale*. A, complete suture of specimen from *Ophiceras (Metophiceras)* Zone from Clavering Island, East Greenland (Spath, 1935, pl. 2, fig. 3b) at whorl height of approximately 75 mm; B, complete suture of specimen from Blind Fiord Formation, Axel Heiberg Island (Tozer, 1961, fig. 7) at a diameter of approximately 90 mm; C, complete suture of *Otoceras indigirense* Popov (1958, fig. 1, 1) from eastern Verkhoyansk region, Kerekhtyakh brook, Siberia, scale uncertain; D, specimen from eastern Verkhoyansk region, Kerekhtyakh brook, Siberia (Popov, 1958, figs. 1, 2), scale uncertain; E, specimen from upper Indigirka River, Verkhoyansk Mountains, Siberia, MCZ 6103, at a diameter of 35 mm; F, specimen identified as *O. indigirense* by Yu. N. Popov from East Khandiga River, Verkhoyansk region, Siberia, MCZ 8685, at a whorl height of 25 mm; G, specimen from upper member of Sadlerochit Formation, Canning River, northern Alaska, at a whorl height of 100 mm; H, paratype of *O. concavum* Tozer (1967, fig. 20) from Blind Fiord Formation, Axel Heiberg Island, northern Canada, at a whorl height of approximately 45 mm.

whorl heights of 50 or more millimeters, while those known in *O. woodwardi* are from much smaller specimens. Adventitious elements in the dorsal saddles of *O. woodwardi* are present at a whorl height of 11.8 mm (Fig. 2A) and are more marked in Diener's specimens (Fig. 2B), which I believe to be taken at a whorl height of 25 mm. It is quite apparent that much more data on the development of dorsal suture in *O. boreale* are needed.

In addition, Spath (1935: 11) noted the larger size of the Arctic forms over those from the Himalayas. Both Spath (1935) and Tozer (1961) stated that they had seen specimens of *O. boreale* probably having a diameter of 300 mm or more. The largest of the Himalayan specimens (Pl. 2, figs. 3, 4) has a diameter of 152 mm.

Finally, Spath (1935: 11) noted that in the lower *Glyptophiceras* beds *Otoceras* was represented by a number of fragmentary and mostly crushed specimens. He had, however, one specimen (Spath, 1935, pl. 3, fig. 4) representing only a part of a whorl which was very inflated in cross section. On this basis he suggested that it was probably not conspecific with *O. boreale*.

Considering the great variability in all

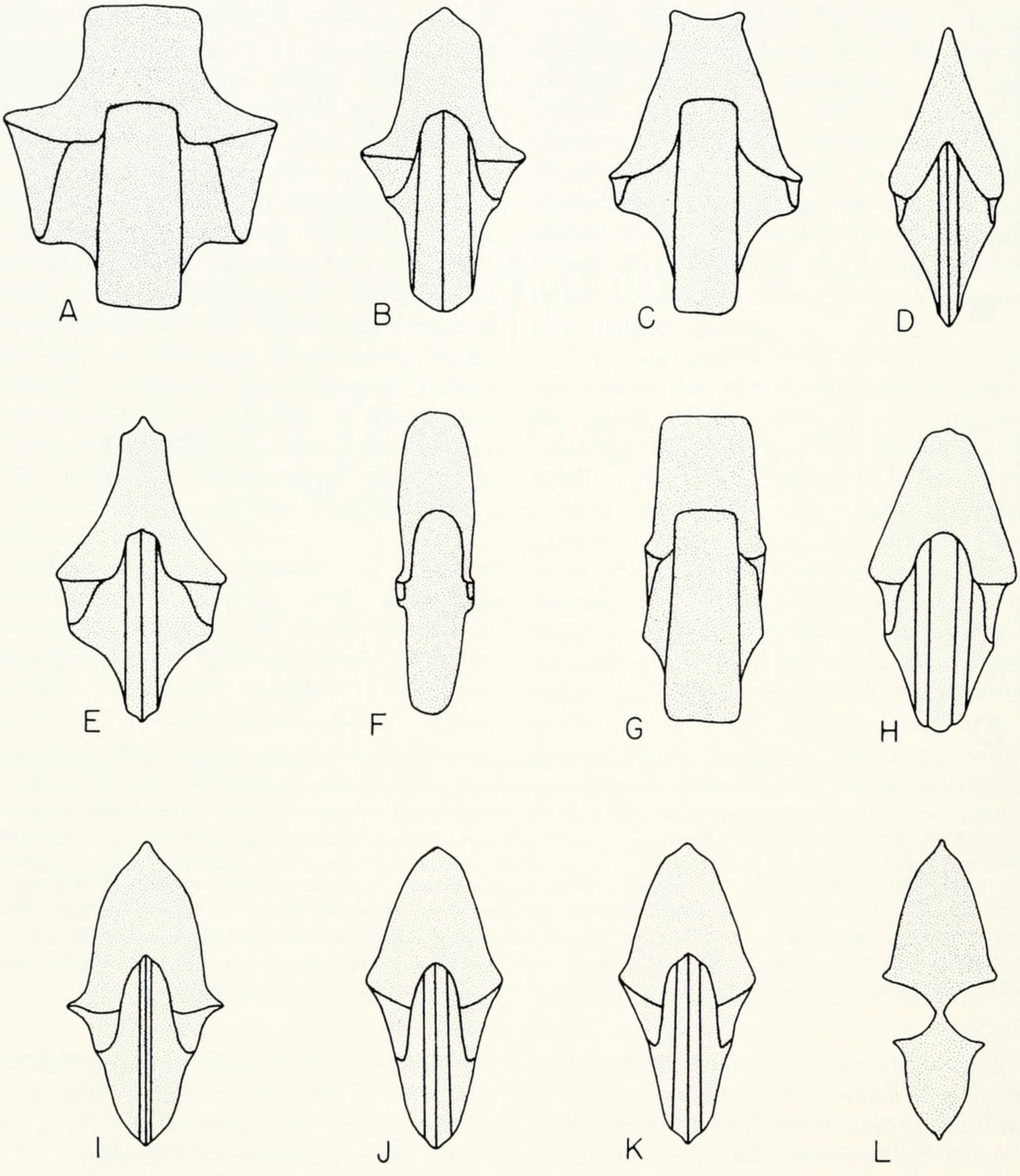

Figure 8. Cross sections of the conch of A, *Araxoceras latissimum* Ruzhentsev, 1959, fig. 1a, diameter 58 mm; B, *Prototoceras tropitum* (Abich), Ruzhentsev, 1959, fig. 1c, diameter 23 mm; C, *Rotaraxoceras caucasium* Ruzhentsev, 1959, fig. 1b, diameter 33 mm; D, *Pseudotoceras djoulfense* (Abich), Ruzhentsev, 1963, pl. 6, fig. 2b, diameter 110 mm; E, *Urartoceras abichanum* Ruzhentsev, 1959 fig. 1g, diameter 75 mm; F, *Dzhulfoceras furnishi* Ruzhentsev, 1962, pl. 5, fig. 1b, diameter 36 mm; G, *Vedioceras ventroplanum* Ruzhentsev, 1962, pl. 5, fig. 3a, diameter 75 mm; H, *Avushoceras jakowlewi* Ruzhentsev, 1962, pl. 5, fig. 5a, diameter 72 mm; I, *Otoceras woodwardi woodwardi*, Diener, 1897, pl. 2, fig. 1b, diameter 140 mm; J, *Otoceras undatum* Griesbach, Diener, 1897, pl. 4, fig. 6b, diameter 40 mm; K, *Otoceras clivei* Diener, 1897, pl. 3, fig. 2b, diameter 40 mm; L, *Otoceras woodwardi borealis* Spath, 1935, pl. 1, fig. 1b, diameter 115 mm.

morphologic features of the Himalayan *Otoceras woodwardi,* the criteria used by Spath (1935) in separating the Arctic forms as a distinct species do not appear to be convincing. It is granted that more data are needed, especially on the Arctic representatives of *Otoceras,* that is, data on variation in shell form, ontogeny, and suture. As known at present, however, it is only in the dorsal suture that consistent differences between the Himalayan and Arctic forms can be observed. This being the case, and considering the fact that the two forms are geographically distinct, I choose to consider the Arctic *O. boreale* as a subspecies of the Himalayan *Otoceras woodwardi.*

The Ancestry of *Otoceras*

It has long been recognized that the Dzhulfian otocerids are closely related to the earliest Triassic *Otoceras woodwardi* (Diener, 1897; Spath, 1930, 1934). However, until recently the relationship has been obscure, as only the few Dzhulfian species described by Abich (1878) were known. One of the most interesting results of the renewed field studies in Soviet Dzhulfa was the discovery of a large and diversified fauna of "otocerids" that have been described by Ruzhentsev (1959, 1962, 1963; Ruzhentsev and Shevyrev *in* Ruzhentsev and Sarycheva, 1965). This fauna now includes nine genera and thirty species brought together in the family Araxoceratidae Ruzhentsev. The family was diagnosed as follows (Ruzhentsev, 1959: Translation by Mrs. Mary L. Davis, University of Iowa): "The shell is from pulley-shaped to disc-shaped. The ventral side is flat, concave, or tectiform, of various widths. All have 14–16 lobes, not counting supplementary ones. The ventral lobe is narrow, poorly dissected, with wedge-shaped branches; by length it is shorter or equal to the primary umbilical lobe. There are not more than two well-developed external umbilical lobes, they have ceratitic crenulations at their base. Out from them to the umbilical suture goes a small wedge-shaped lobe, the quantity, form, and situation of which are highly changeable. The dorsal lobe is narrow, long, bifid. The inner lateral lobe is narrow and wedge-shaped. The inner umbilical lobes are one or more; they are also wedge-shaped." Ruzhentsev placed the following genera in this family: *Araxoceras* Ruzhentsev, 1959; *Rotaraxoceras* Ruzhentsev, 1959; *Urartoceras* Ruzhentsev, 1959; *Prototoceras* Spath, 1930; *Pseudotoceras* Ruzhentsev, 1962; *Vescotoceras* Ruzhentsev, 1962; *Dzhulfoceras* Ruzhentsev, 1962; *Vedioceras* Ruzhentsev, 1962; and *Avushoceras* Ruzhentsev, 1962. This family includes ammonoids with a bewildering array of shell shapes (Fig. 8). The whorl sections vary from forms with flat venters (*Araxoceras, Vedioceras*), to forms with fastigate venters, some broad, some narrow (*Prototoceras, Urartoceras, Pseudotoceras*), to forms with rounded venters (*Dzhulfoceras, Avushoceras*). All genera are involute and some have prominent flared umbilical rims (*Araxoceras, Urartoceras, Prototoceras*). The sutures, though varying in detail from one genus to the other, have the same basic pattern (Fig. 9).

The apparent sudden appearance of this large diversified fauna of "otocerids" in the late Permian Dzhulfian strata is a puzzle. Ruzhentsev (*in* Ruzhentsev and Sarycheva, 1965) suggested that the radiation of the Araxoceratidae was made possible by the great decline among the agoniatites and goniatites. While he believed that the Araxoceratidae were endemic to the general Dzhulfian region, it is now known that the family is quite widely distributed. Stepanov, Golshani, and Stöcklin (1969) recorded the presence of *Araxoceras, Vescotoceras, Vedioceras, Pseudotoceras,* and *Avushoceras* from the Julfa beds at Kuh-e-Ali Bashi, northwestern Iran. Recently Taraz (1969) listed *Prototoceras, Vescotoceras,* and *Pseudotoceras* from upper Permian strata near Abadeh in central Iran. In the overlying unit from which Taraz

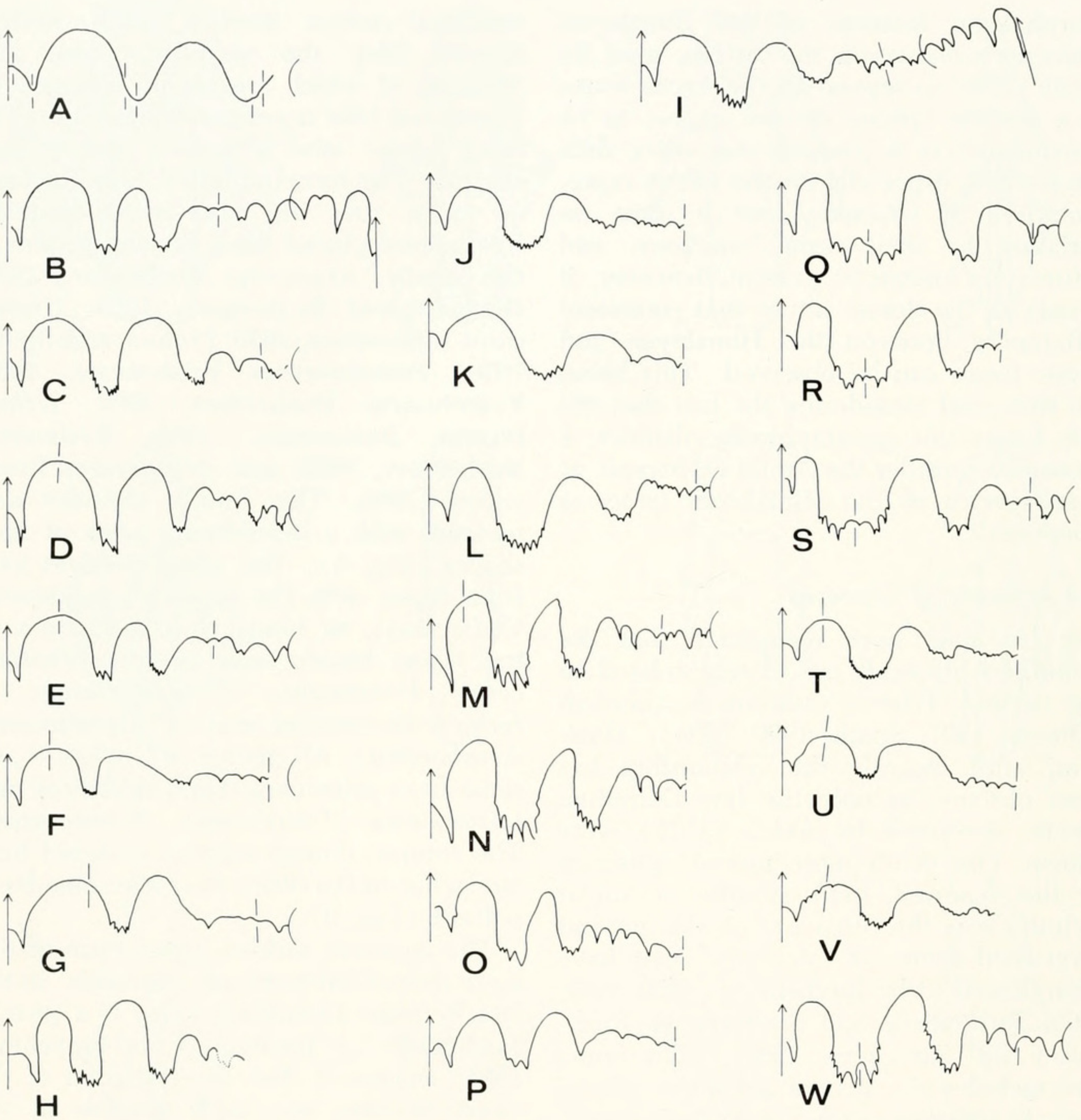

Figure 9. Diagrammatic representation of the suture of A, *Glyphioceras (Anderssonoceras) anfuense* Grabau (1924, fig. 301), holotype, at diameter of approximately 20 mm; B, *Araxoceras latissimum* Ruzhentsev, 1959, fig. 2a; C, *Araxoceras glenisteri* Ruzhentsev, 1962, fig. 2d; D, *Araxoceras latum* Ruzhentsev, 1962, fig. 2b; E, *Araxoceras latissimum* Ruzhentsev, 1962, fig. 2a; F, *Rotaraxoceras caucasium* Ruzhentsev, 1962, fig. 4a; G, *Rotaraxoceras deruptum* Ruzhentsev, 1962, fig. 4b; H, *Pseudotoceras armenorum* Ruzhentsev, 1962, fig. 6; I, *Prototoceras tropitum* (Abich), Ruzhentsev, 1959, fig. 2c; J, *Prototoceras acutum* Ruzhentsev, 1959, fig. 2d; K, *Prototoceras parallelum* Ruzhentsev, 1959, fig. 2e; L, *Discotoceras raddei* (Arthaber), Ruzhentsev, 1959, fig. 2f; M, *Urartoceras abichianum* Ruzhentsev, 1962, fig. 5; N, *Urartoceras abichianum* Ruzhentsev, 1959, fig. 2g; O, *Dzhulfoceras furnishi* Ruzhentsev, 1962, fig. 8a; P, *Dzhulfoceras paulum* Ruzhentsev, 1962, fig. 8b; Q, *Vedioceras ogbinense* Ruzhentsev, 1962, fig. 10c; R, *Vedioceras ventroplanum* Ruzhentsev, 1962, fig. 10b; S, *Vedioceras ventroplanum* Ruzhentsev, 1962, fig. 10a; T, *Vescotoceras acutum* Ruzhentsev, 1962, fig. 7a; U, *Vescotoceras evanidum* Ruzhentsev, 1962, fig. 7c; V, *Vescotoceras serratum* Ruzhentsev, 1962, fig. 7b; W, *Avushoceras jakowlewi* Ruzhentsev, 1962, fig. 10d.

(1969: 691) records *Pseudogastrioceras, Dzhulfites, Bernhardites, Abichites,* and *Paratirolites,* Curt Teichert was able to collect a small fauna including not only several of these genera but also a specimen of *Vedioceras.* Chao (1965) recorded *Prototoceras, Araxoceras,* and *Vescotoceras* from the Laoshan shale member of the Loping coal series of Kwangsi, South China. The family is now also known from the western hemisphere. Spinosa, Furnish, and Glenister (1970) have described a new genus, *Eoaraxoceras,* from strata of uppermost Guadalupian age from the La Colorado beds of Valle de las Delicias, Coahuila, Mexico, an occurrence that is presumably older than that of Soviet Dzhulfa, Abadeh, and South China.

The phylogenetic relations of the various genera of the Araxoceratidae are by no means understood. The data on the South China fauna are still of a preliminary nature and are of no help to the present problem. Another difficulty is that the preservation of many Dzhulfa and Kuh-e-Ali Bashi specimens leaves much to be desired. The specimens are internal casts, and many are fragmentary and crushed, at least on one side. The inner whorls are filled with coarse crystalline calcite and are commonly deformed. The significance of the stratigraphic distribution of the genera at Soviet Dzhulfa is uncertain at this stage. *Araxoceras* and *Vescotoceras* appear to be confined to the *Araxoceras* beds; *Urartoceras, Dzhulfoceras, Vedioceras,* and *Avushoceras* are confined to the overlying *Vedioceras* beds; but *Rotaraxoceras, Prototoceras,* and *Pseudotoceras* are present in both the *Araxoceras* and *Vedioceras* beds (Ruzhentsev and Sarycheva, 1965: 48).

Ruzhentsev's (1959) conclusion that the ancestral form of the Araxoceratidae is *Glyphioceras* (*Anderssonoceras*) *anfuense* Grabau (1924) appears to be well founded. Ruzhentsev (1959) established the family Anderssonoceratidae for the single genus *Anderssonoceras.* The pattern of radiation within the Araxoceratidae is not at all understood. In his first paper on this family Ruzhentsev (1959) considered the then known araxoceratids to be divisible into three groups: (1) *Araxoceras* and *Rotaraxoceras,* (2) *Prototoceras* and *Discotoceras,* and (3) *Urartoceras.* He considered each of these groups to be an independent development from an unknown genus with ceratitic lobes close in form to *Anderssonoceras.* The genus *Eoaraxoceras* Spinosa et al. (1970) appears to be such a form. Ruzhentsev (1959) suggested that the Triassic *Otoceras* was derived from the *Prototoceras-Discotoceras* group. Continued study of additional collections from Soviet Dzhulfa led to the recognition of a number of new genera and species (Ruzhentsev, 1962, 1963). With this great increase in data on the araxoceratids, Ruzhentsev (1962, and Ruzhentsev *in* Ruzhentsev and Sarycheva, 1965) came to the conclusion that the immediate ancestor of *Otoceras* was *Pseudotoceras.* With this conclusion I completely agree. *Pseudotoceras* has a simpler suture with fewer lobe elements and lacks the flaring of the umbilical rim (Figs. 8D, I).

There is one other genus of the Otoceratidae that needs comment and this is *Anotoceras* Hyatt (1900: 553; type species *Prosphingites nala* Diener, 1897: 54, pl. 1, fig. 4). This is a relatively rare form from the *Otoceras-Ophiceras* beds of the Himalayas. Diener (1897) had only seven specimens available for study and of these only four are still preserved in the Geological Survey of India collections in Calcutta. I have seen the Eigil Nielsen collection from the *Otoceras-Ophiceras* beds at Muth which contains only one fragmentary phragmocone of *Anotoceras.* In addition to the species selected as type for this genus Diener (1897) described another species, *Anotoceras kama,* that was differentiated on the basis of a fastigate venter (Pl. 12, figs. 13, 14). My own examination of this specimen showed that it is slightly crushed, mainly along the venter. In all other aspects it resembles specimens of *Anoto-*

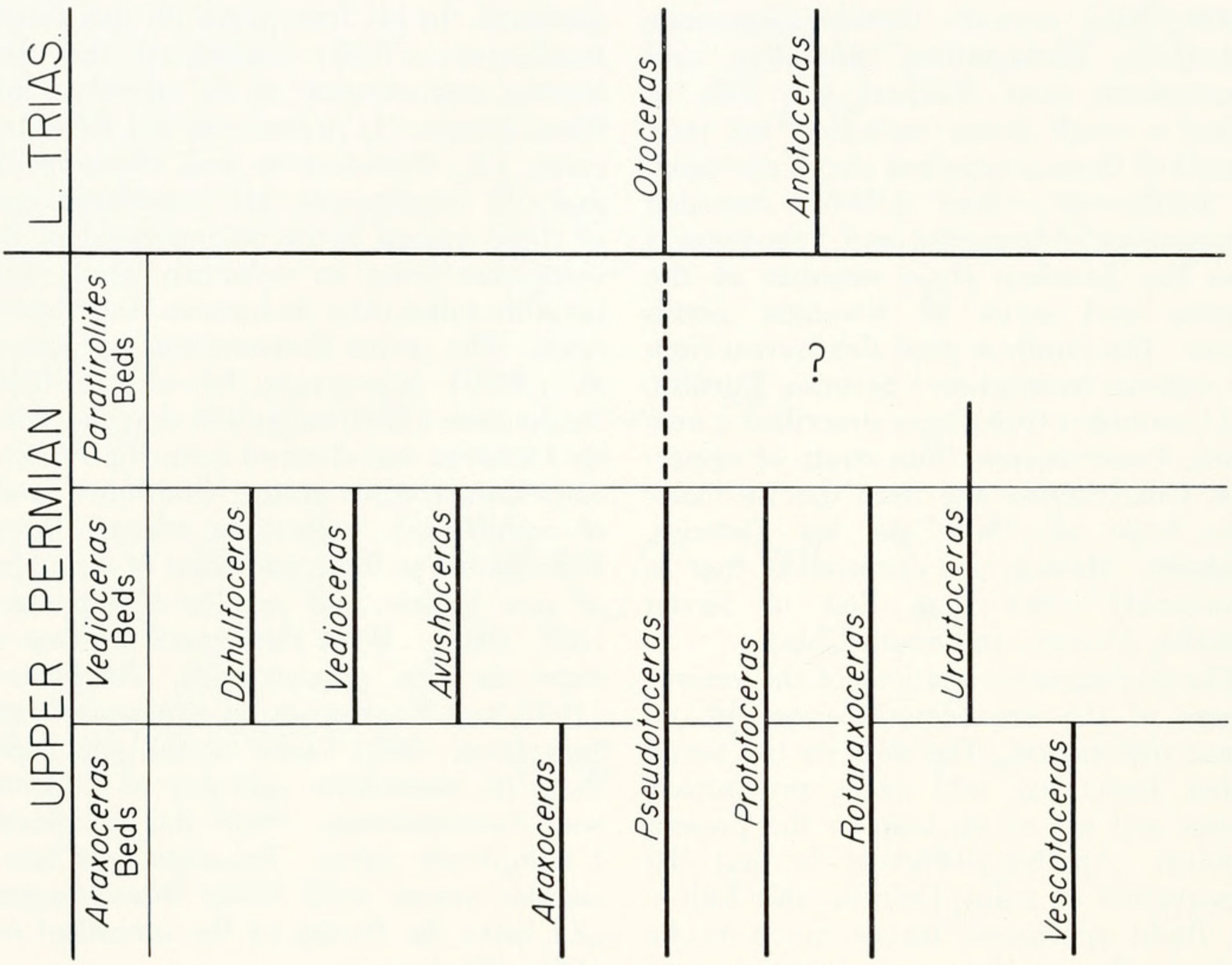

Figure 10. Suggested phylogenetic relations of late Permian and early Triassic genera of family Otoceratidae.

ceras nala, as already noted by Diener (1897: 56). Spath (1930: 7) established the species *Anotoceras intermedium* for one of the figured paratypes of *Anotoceras nala* (Diener, 1897, pl. 7, fig. 13; Pl. 12, figs. 9, 10 of this report). This specimen is slightly broader but does not differ in whorl section nor in the umbilical rim as suggested by Spath. I believe neither of these criteria to be of specific significance. As now understood, *Anotoceras* is a monotypic genus, known only from the *Otoceras-Ophiceras* beds of the Himalayas, on which data are extremely incomplete. For the time being I am inclined to follow Spath (1934: 70), who concluded that the genus "may, however, be retained in the present family [Otoceratidae] for reduced otoceratids with open umbilicus and rounded venter." There is, however, no clue as to where one could identify the ancestral form within the araxoceratids.

In spite of the uncertainty of the position of *Anotoceras* the relationships of *Pseudotoceras* and *Otoceras* (ancestor-descendant) are very impressive, especially when one considers that the differences between these genera are only the result of evolutionary changes along certain adaptive lines—conch form and suture. Another important feature to point out here is that *Otoceras* survived only during the lowest Scythian (Lower Triassic) zone. Considering its fairly close relationship to *Pseudotoceras* it does not seem reasonable to separate *Otoceras* in a family distinct from that of its late Permian ancestor. All the araxoceratids and *Otoceras,* plus *Anotoceras,* comprise a single unified family group (Fig. 10). The great radiation of this group is a characteristic feature of late Permian time. The genus *Otoceras* is the only member of the group that survived into early Triassic time. This genus, aside from its presence in the Himalayas, became widely distributed in the circum-Arctic region. *Otoceras* is the terminal member of a diverse and unique ammonoid family. The family Araxoceratidae Ruzhentsev (1959) should be included in the Otoceratidae Hyatt (1900).

Otoceras as a Zone Fossil

The *Otoceras-Ophiceras* beds of the Himalayas have long been recognized as representing the basal Triassic biostratigraphic zone. Diener (1912) thoroughly reviewed the data and the evolution of thought on its stratigraphy and fauna. His concluding remarks summarize quite well the accepted view (Diener, 1912: 32): "Thus the fauna of the *Otoceras* stage represents one single palaeontological zone only, which, from its most conspicuous types, should be called zone of *Otoceras Woodwardi* and *Ophiceras Sakuntala*."

The *Otoceras-Ophiceras* beds of the Spiti and Painkhanda regions in the Himalayas are approximately one meter thick (Diener, 1912). The lower and upper thirds of this unit are abundantly fossiliferous. At Spiti, *Otoceras* is confined to the lower third of this unit; but in Painkhanda, 130 miles to the southeast, *Otoceras* is present in both the lower and upper thirds of the unit. Species of *Ophiceras* are the predominant elements in the lower and upper thirds of this unit. This difference in representation of *Otoceras* and *Ophiceras* in the lowest Scythian unit of the Himalayas is well documented in the numbers of specimens of each species from nine collections studied by Diener (1897) (Table 1). It is clear from these data that *Ophiceras* is by far the predominant element, and *Otoceras* the second-ranking element in the ammonoid fauna.

Discussion of this biostratigraphic zone for the Himalayas has centered primarily on *Otoceras* and *Ophiceras*. Strangely there has been little discussion of the six other genera described from this fauna by Diener (1897), namely: *Episageceras, Glyptophiceras, Proptychites, Vishnuites, Prionolobus,* and *Anotoceras,* which was discussed previously. Noetling (1901) questioned the accuracy of the horizon from which some of the specimens assigned to these genera were claimed to have come. It should be recalled that in the first monograph on the fauna of the Himalayan Lower Triassic (Diener, 1897), the *Otoceras-Ophiceras* and *Meekoceras* faunas were not differentiated. In the second monograph (v. Krafft and Diener, 1909) the *Otoceras-Ophiceras* faunas and the *Meekoceras* faunas were clearly differentiated. In that monograph Diener (*in* v. Krafft and Diener, 1909: 164) discussed this point and presented a list of those species which he considered "with full certainty" as belonging to the *Otoceras-Ophiceras* Zone. The list of these species is given in Table 1. He reaffirmed his conclusion at a later date (Diener, 1912: 23).

It is appropriate to review the data on each of these genera. The only genus that appears to have passed through the Permo-Triassic threshold is *Episageceras,* type species: *Sageceras* (*Medlicottia*) *wynnei* Waagen (1880) from the Upper Permian of the Salt Range. Species of this genus have also been recorded from the Ambilobe beds of northern Madagascar associated with *Cyclolobus* (Treat, 1933) and from Timor (Haniel, 1915; Wanner, 1932). In the Spiti region of the Himalayas, *Episageceras dalailamae* Diener occurs in the lowest five-inch bed (Fig. 11), along with *Otoceras, Anotoceras,* and *Ophiceras* (Diener, 1912: 17). In Painkhanda this same species is known from a fragment in the main layer of *Otoceras* (Fig. 11, bed 1) and by a well-preserved, nearly complete specimen from bed 2 associated with *Proptychites scheibleri* Diener. These two specimens were collected personally by

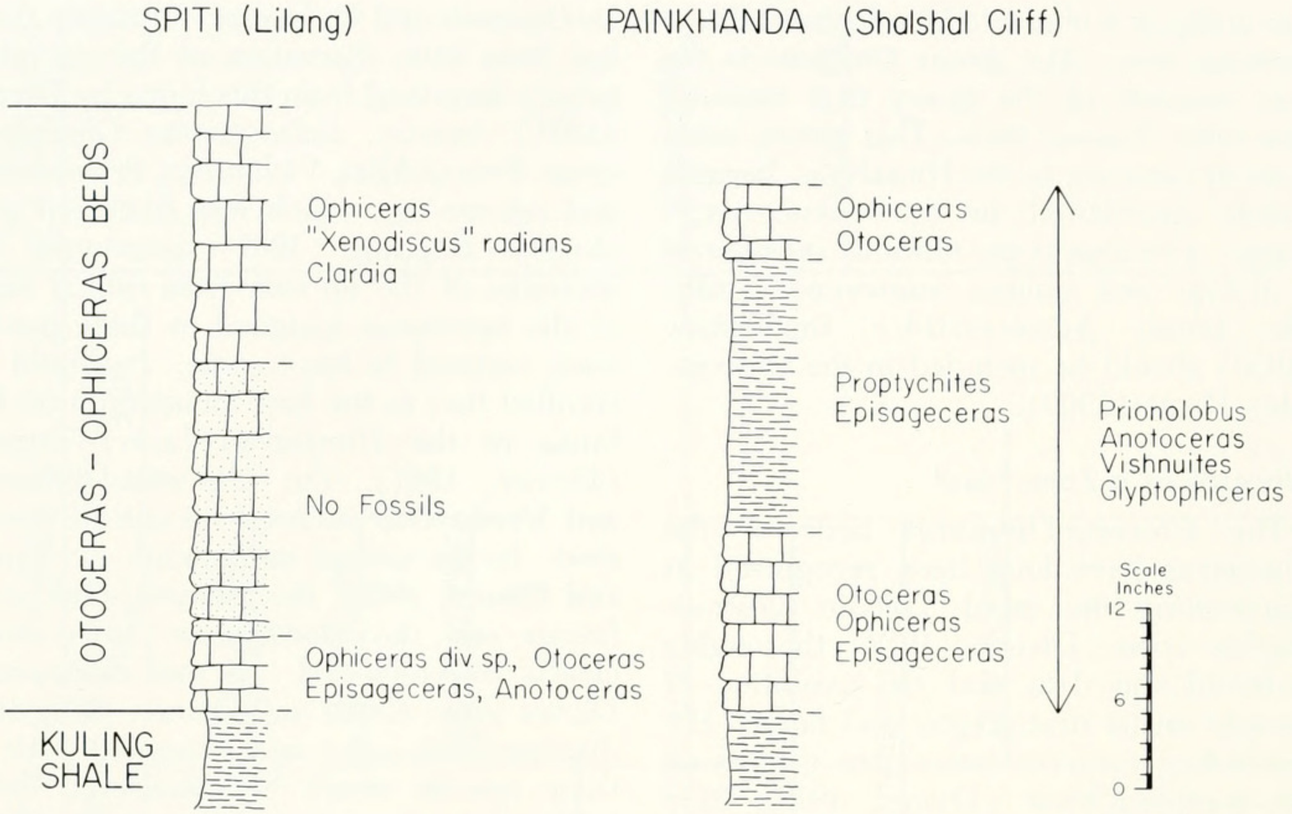

Figure 11. Stratigraphic section of *Otoceras-Ophiceras* beds at Spiti (Lilang) and Painkhanda (Shalshal Cliff), Himalayas. (Data from Diener, 1912.)

Diener (Diener, 1897: 59) and are illustrated here on Plate 11, figures 1–4.

The single specimen assigned to *Ophiceras himalayanum* Griesbach (1880: 111, pl. 3, fig. 8) and discussed in more detail by Diener (1897: 41, pl. 14, fig. 14) is a species of *Glyptophiceras*. This species is based on a single specimen embedded in a slab of rock adjacent to a specimen of *Otoceras woodwardi* (Pl. 11, fig. 7). A single specimen from the Dolomite unit of the Kathwai Member of the Mianwali Formation in the Salt Range of west Pakistan is believed to be conspecific with Griesbach's type specimen (Kummel *in* Kummel and Teichert, 1970).

Proptychites scheibleri Diener (1897: 79, pl. 6, fig. 3; Pl. 11, figs. 5, 6 of this report) was established on a single specimen collected by Diener in 1892 from bed 2 of the *Otoceras-Ophiceras* beds (Fig. 11) at Shalshal Cliff. Diener (1912: 23) made particular stress of the fact that he personally collected this specimen. The same bed at Shalshal Cliff yielded only one other specimen of ammonoid, *Episageceras dalailamae* Diener. This is the oldest species of the genus *Proptychites*, but the genus is extensively distributed in the remaining lower half of the Scythian.

Another rare ammonoid in the *Otoceras-Ophiceras* beds at Shalshal is *Vishnuites pralambha* Diener. This is a compressed form with an acute venter. Diener (1897) had available two specimens that are illustrated here on Plate 12, figures 1–4. Unfortunately, there are no data as to the precise level within the *Otoceras-Ophiceras* beds from which these specimens were collected.

The stratigraphic position of *Meekoceras hodgsoni* Diener had been a source of intense debate between Noetling (1901) and Diener (1901). Noetling maintained that the type specimen must have come from the overlying *Meekoceras* beds and Diener held to his original position that it came from the *Otoceras-Ophiceras* beds. Von

Krafft (*in* v. Krafft and Diener, 1909: 26) redescribed Diener's type specimen and was able to demonstrate that the venter was truncate to the earliest diameter of the specimen. In that same monograph, Diener described and illustrated a specimen in von Krafft's collection from the *Otoceras* beds at Shalshal that he believed to be a new example of *Meekoceras hodgsoni*. In his comments on that specimen Diener (*in* v. Krafft and Diener, 1909: 28) again discussed the stratigraphic position of this species as follows: "A. v. Krafft was, however, mistaken, when he spoke of the absence of any new examples of *Meekoceras hodgsoni* in Noetling's and his own collections. Among his collection from the *Otoceras* beds of the Shalshal Cliff I found a well-preserved specimen of *Meekoceras*, marked on the label as *Meekoceras* sp. ind., Shalshal Cliff near Rimkin Paiar E. G., *Otoceras* beds, found along with *Ophiceras*. That both specimen and label actually belong together is indisputable both being marked with figures K 10, 859.

"This specimen, which has been figured on Pl. XXX, Fig. 1 (Pl. 12, figs. 7, 8 of this report) cannot be separated specifically from *Meekoceras Hodgsoni*, with which it agrees in all its characters of specific importance. I wish to draw the special attention of the reader to the remarkable narrowness of the external area and to the compressed shape of the whorls in general, two leading features in *Meekoceras Hodgsoni*.

"The discovery of a specimen of *Meekoceras Hodgsoni* in the *Otoceras* beds (*sensu stricto*) is of great stratigraphical interest. It fully confirms my statement (Centralblatt f. Miner, etc., 1901, p. 656) that my type specimen had been collected in the *Otoceras* beds of the Shalshal cliff and not in the horizon of *Meekoceras Markhami*, as had been suggested by Noetling. But even if the identification of the present specimen with *Meekoceras Hodgsoni* should be questioned, the presence of a true *Meekoceras* in the *Otoceras* beds of Painkhanda would remain an indisputable fact, in contradiction to what has been suggested by Noetling as to the first appearance of this genus in the Himalayas."

I have had the opportunity of examining the collection of Permian and Triassic fossils from the Spiti area assembled by Eigil Nielsen, formerly of the Universitetets Mineralogiske og Geologiske Museum, Copenhagen. The largest collection came from Muth in Spiti and this contains five specimens of *Meekoceras hodgsoni* bearing labels as coming from the *Otoceras-Ophiceras* beds.

Before discussing the genus *Ophiceras*, which is by far the predominant form in the *Otoceras-Ophiceras* beds, we need to consider *Xenodiscus radians*, von Krafft, *non* Waagen (*in* v. Krafft and Diener, 1909, p. 95, pl. 25, fig. 2; Pl. 12, fig. 15 of this report). In discussing the horizon of the specimens he assigned to *Xenodiscus radians*, von Krafft stated that most of the specimens came from the *Meekoceras* beds at various localities in the Spiti region and a few were listed with question as from the *Otoceras* beds. Diener, however, added a footnote to those statements (*in* v. Krafft and Diener, 1909: 95) as follows: "One specimen from A. v. Krafft's own collection —illustrated on Pl. XXV, fig. 2 (Pl. 12, fig. 15 of this report)—is marked on the accompanying label in A. v. Krafft's handwriting: 'Lilang, Spiti, horizon of *Ophiceras Sakuntala*.' This would prove the specimen to have been found in the *Otoceras* beds S. S." *Xenodiscus radians* von Krafft (*non* Waagen) appears to be a species of *Xenodiscoides*.

Finally, there is the genus *Ophiceras*, which has been somewhat overshadowed by the attention investigators have paid to the genus *Otoceras*. Diener, throughout his writings on the Lower Triassic ammonoids of the Himalayas, has emphasized the predominance of *Ophiceras* in the lowest Triassic beds. In his first monograph on this fauna, Diener (1897) had approximately 400 specimens from these beds of which roughly 330 were species of *Ophiceras* (Table 1). Diener (1897: 100) began his discussion of the genus *Ophiceras* in the following fashion: "The forms which will be described in the following pages under the generic designation proposed by C. L. Griesbach, surpass enormously, in number of individuals, all the other members of the Cephalopoda, which are contained in the geologically oldest strata of the Himalayas, *viz.*, the *Otoceras* beds. All these forms appear at first sight to be linked together most intimately by similarity of shape and sutural lines. Groups of forms, it is true, may be distinguished among them, without great difficulty, which owing to remarkable characters seem to constitute excellent species, but a closer examination most conclusively shows that even groups, the typical form of which seems to be widely different, are connected by transitional forms with such different characters, that it is scarcely possible to identify them with either the one or the other species." This statement expresses well the great plasticity of this stock. Diener (1897: 104) stated his taxonomic philosophy on the genus as follows: "The genus *Ophiceras* is represented in the Himalayas by ten species, which may most conveniently be arranged in groups according to the differences in sculpture. One group of forms, which is closely allied to *O. tibeticum* Griesbach is distinguished by a sculpture, which consists of strong falciform folds and knob-like elevations, but which are not as distinctly demarcated as the tubercles in the *Trachyostraca.* In the other group the surface of the shell is either perfectly smooth or covered with low and broad falciform folds. This group is named from the most common species of the genus *O. Sakuntala.* It must be borne in mind, however, that a distinct boundary does not exist between the two groups, and that, even in species with a strongly developed sculpture, transitional forms occur, which point to the most intimate connection of the different varieties, among which the most prominent ones have been singled out as prototypes of my species." Diener (1897: 104) then classified the species of *Ophiceras* as follows:

Group of *Ophiceras tibeticum* Griesbach
Ophiceras tibeticum Griesbach
" *gibbosum* Griesbach
" *serpentinum* Diener
" *platyspira* Diener
Group of *Ophiceras Sakuntala* Diener
Ophiceras sakuntala Diener
" *medium* Griesbach
" *ptychodes* Diener
" *demissum* Oppel
" *chamunda* Diener
" *dharma* Diener

At a later date, Diener (*in* v. Krafft and Diener, 1909: 164) revised the list by excluding *Ophiceras dharma*, as the geological horizon of this sample was uncertain. At the same time he added *Ophiceras stricturatum* Frech and Noetling.

The only specimens studied by Diener that are still available are those figured in his monograph (Diener, 1897). As these figures are all line drawings, photographs of these specimens are reproduced here on Plates 5 to 10. There are only 42 figured specimens, which is a small sample of the more than 300 specimens that were available to Diener. In the discussion of each of these species Diener (1897) devoted much attention to variation within his species and forms transitional to others of his species. Considering the stratigraphic placement of the specimens, the fact that a large part of the samples came from one locality, Shalshal, and the nature of the variation discussed by Diener and also shown to some extent in the figured specimens, I cannot believe the genus is represented by ten species. It seems more reasonable that the fauna includes no more than two or three species. A suggested regrouping of these species is represented in the legends of Plates 5 to 10.

Regardless of whether one considers

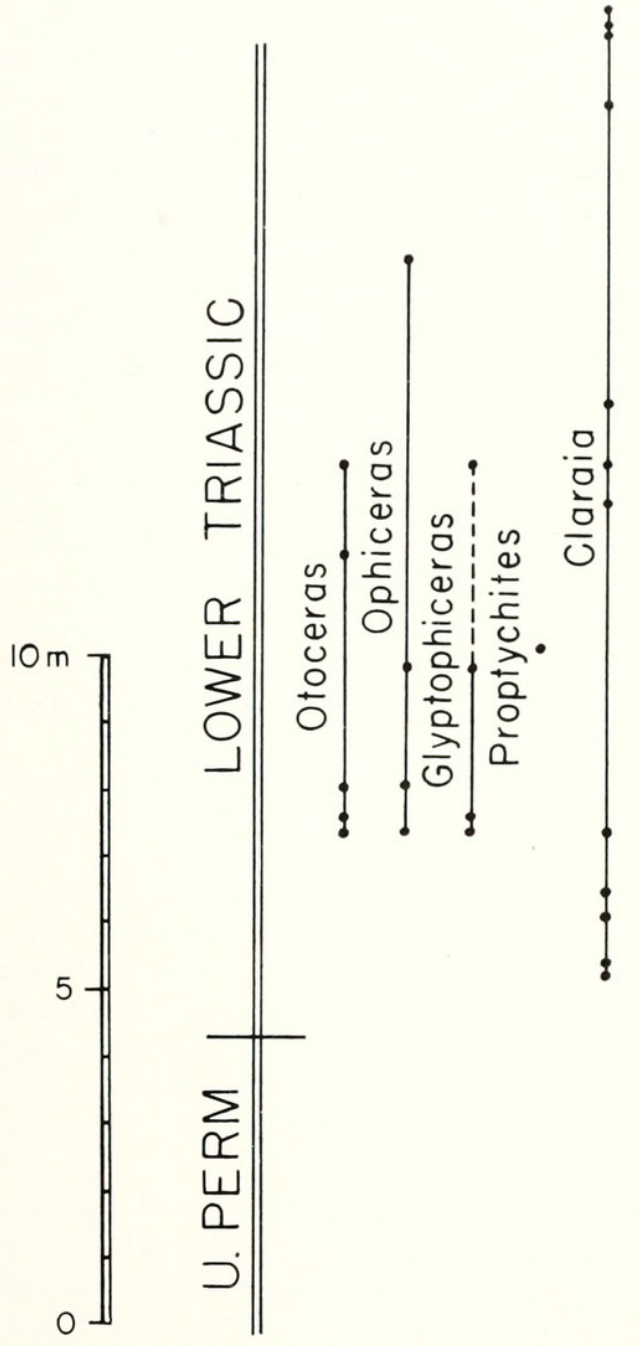

Figure 12. Stratigraphic range of ammonoid genera and the bivalve *Claraia* at Guryul Ravine, Kashmir. (Data from Nakazawa et al., 1970.)

Ophiceras in the Himalayas to include a few or many species, it is clear that the genus was undergoing a very extensive evolutionary radiation. None of the other genera of the *Otoceras-Ophiceras* beds show any comparable speciation. This fact has been almost completely overlooked in the numerous discussions on the Permo-Triassic boundary in the Himalayas. Diener, in his summary paper on the Triassic of the Himalayas (Diener, 1912), centers his discussion of this problem predominantly on *Otoceras*. It has been shown in the previous chapters that *Otoceras* is the last surviving element of a family that underwent a broad-scale radiation in the late Permian. In addition, the genus *Otoceras* is believed to be represented by a single species and two subspecies. This is in great contrast to what we can see for *Ophiceras*.

Nakazawa et al. (1970) have contributed significant new data on the *Otoceras-Ophiceras* Zone in the Himalayas. Very detailed stratigraphic measurements and collecting of lowest Triassic formations exposed in Guryul Ravine, near Srinagar, Kashmir, show that in the beds containing *Otoceras* there also occur *Ophiceras*, *Glyptophiceras*, and *Proptychites*. A summary of their ammonoid distribution data is shown in Figure 12.

It was pointed out above that *Otoceras boreale* of the circum-Arctic region is considered to be a subspecies of the Himalayan *Otoceras woodwardi* and is known from Siberia, Spitsbergen, East Greenland, Arctic Canada, and northern Alaska.

There is one other reported occurrence of *Otoceras*. Hsu (1937) has described and illustrated two poorly preserved, crushed specimens, one of which preserved much of the suture, from Chinglung Limestone at Chinglungshan near Nanking. The stratigraphy of this area and field data on this specimen were described by Chi, Hsu, and Sheng (1937). The specimen illustrated by Hsu (1937, pl. 2, fig. 2) shows a tri-carinate venter and indication that the umbilical area was flared. The second specimen was illustrated only by its suture, which appears simplified. Though the specimen is completely crushed, the character of the venter, umbilical region, and the suture strongly suggests that the generic assignment is not unreasonable. In addition Chi, Hsu, and Sheng (1937) show these two specimens as coming from a one-meter bed of yellowish gray, micaceous

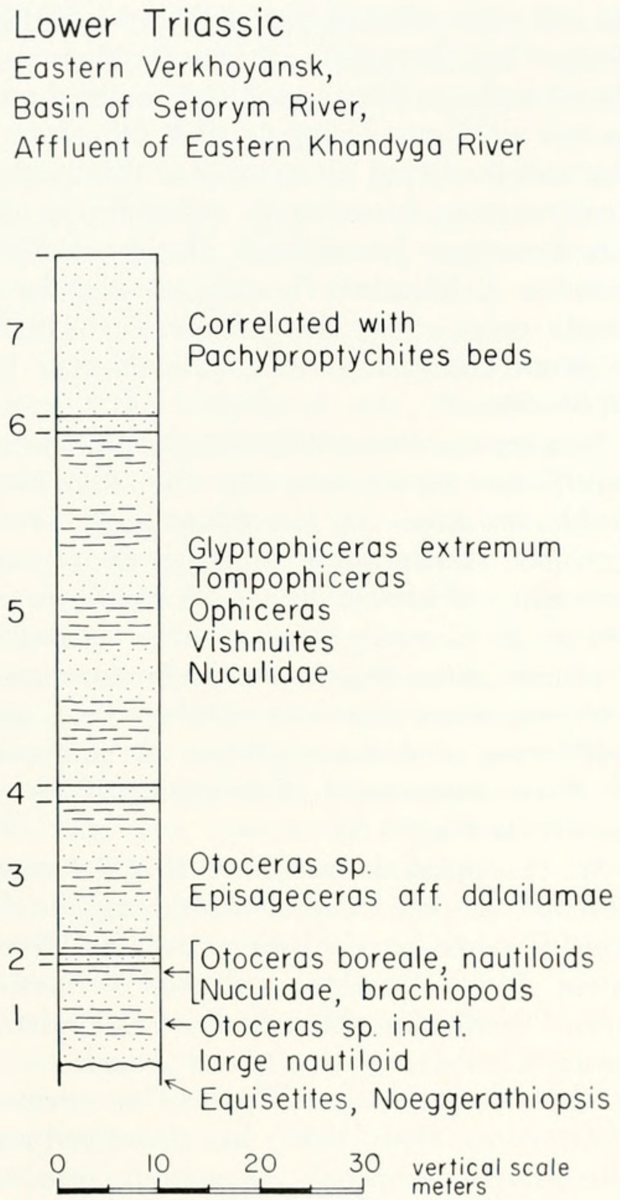

Figure 13. Detailed stratigraphic sections with fossil horizons of lowest Triassic strata in a part of Siberia. (Data kindly furnished by A. N. Oleynikov, VSEGEI, Leningrad.)

shale that is separated from the Lungtan coal series containing a *Gigantopteris* flora by a covered zone of eight meters. This record of *Otoceras* will remain questionable until additional data become available.

The presence of *Otoceras* in Siberia was first reported by Popov (1958) from the eastern Verkhoyansk region. No data are given in that paper as to the thickness and nature of the sediments. However, Popov (personal communication to the author) writes that the beds with *Otoceras* that he described also contain *Ophiceras, Glyptophiceras, Tompophiceras,* and *Episageceras.* In the summer of 1970 Dr. L. V. Kiparisova led a team of geologists to examine the Permian-Triassic boundary beds in the basin of the Setorym River in the eastern Verkhoyansk region. Dr. A. N. Oleynikov has kindly furnished me with data on the stratigraphic succession and faunal associations for that region, summarized here on Figure 13. In that section *Otoceras* is found within the lower 20 meters of the section. In an overlying bed approximately 35 m in thickness the ammonoid fauna includes *Glyptophiceras, Tompophiceras, Ophiceras,* and *Vishnuites.* Above this are strata correlated with the *Pachyproptychites* beds of that region. For Spitsbergen all we know is the presence of *Otoceras.*

The lowest Triassic is well represented in East Greenland by richly fossiliferous strata well documented by Spath (1930, 1935) and Trümpy (1969). Spath recognized a sequence of beds which are from bottom to top as follows: *Glyptophiceras* beds, *Ophiceras* beds, and the *Vishnuites* beds. The species recognized from these beds by Spath (1935) are as follows:

Glyptophiceras Beds:
- *Otoceras* sp. ind.
- *Ophiceras*? sp. ind.
- *Glyptophiceras triviale*
- *Glyptophiceras polare*

Ophiceras Beds:
- *Otoceras boreale*
- *Ophiceras greenlandicum*
- " (*Lytophiceras*) *commune*
- " " *subsakuntala*
- " " aff. *ptychodes*
- " " *ligatum*
- " " *chamunda*
- " " *kilenense*
- " (*Discophiceras*) *kochi*
- " " *compressum*
- " " *wordiei*
- " " *subkyokticum*
- " (*Metophiceras*) *subdemissum*

" " *noe-nygaardi*
" " *praecursor*
" (*Acanthophiceras*) *poulseni*
Vishnuites (*Paravishnuites*) *oxynotus*
" " *striatus*
Glyptophiceras pseudellipticum
" *gracile*
" *serpentinum*
" *nielseni*
" *pascoei*
" *subextremum*
" *extremum*

Vishnuites Beds:
Ophiceras transitorium
" *kilenense*
" *ultimum*
" *dubium*
" *vishnuoides*
" *leptodiscus*
" (*Acanthophiceras*) *subgibbosum*
Vishnuites wordiei
" *decipiens*
Proptychites grandis
" *subdiscoides*
" (*Koninckites*?) sp. ind.

Spath tended to conceive ammonoid species in very narrow terms and this is especially true of his study of these East Greenland faunas. For the immediate purpose this is of no concern, as it is the sequence and association of genera which is of primary concern. Trümpy (1969: 86) recommended raising *Paravishnuites* to full generic rank primarily on the basis that *Vishnuites* and *Paravishnuites* are derived from different stocks within *Ophiceras* and that the Himalayan *Vishnuites* are not directly related to those from East Greenland, but rather are homeomorphs. The point was also made that *Vishnuites* of the *decipiens* and *wordiei* type were younger than *Paravishnuites*. However, Spath (1935, pl. 12, fig. 3) illustrated a specimen he assigned to *Vishnuites* sp. nov. aff. *wordiei* that came from the same horizon as his two species of *Paravishnuites*, that is, the Upper *Ophiceras* beds. I readily recognize that compressed forms with fastigate venters are often (generally) polyphyletic, but, in this particular instance, I do not think sufficient data are as yet available to make a convincing case. I believe it best for the moment to place all these compressed forms with fastigate venters in a single genus *Vishnuites*.

Schindewolf (1954), Tozer (1967, 1969), and Trümpy (1969) interpret *Metophiceras* as being generically distinct from *Ophiceras*. In fact the first two of these authors believe *Metophiceras* to be a member of the *Xenodiscidae*, primarily on slight differences in the suture. It appears equally plausible that *Metophiceras* is part of the general ophiceratid radiation tending toward a more evolute conch and slightly simpler suture. I am following Spath (1935) in considering *Metophiceras* to be a subgenus of *Ophiceras*.

The lowest Scythian strata of East Greenland thus contain five genera of ammonoids, namely *Otoceras*, *Ophiceras*, *Vishnuites*, *Glyptophiceras*, and *Proptychites*. The genus *Otoceras* is present only in the *Glyptophiceras* beds and the *Ophiceras* beds. Tozer (1967: 16) has made the following comment on the range of *Otoceras* in the *Ophiceras* beds of East Greenland: "Spath (1935, p. 11) records *Otoceras boreale* from the Upper *Ophiceras* beds, but no specimens from this level were illustrated, and according to Dr. Trümpy (written communication, 1966) it is probable that *Otoceras boreale* is restricted to the Lower *Ophiceras* beds . . ." These authors apparently overlooked the specimen Spath (1935) figured on his plate 1, figure 6 that is stated to have come from the *Ophiceras commune* Zone (= Upper *Ophiceras* beds). It was stated above that Curt Teichert and I have two good specimens of *Otoceras woodwardi boreale* from the *Glyptophiceras* beds at Kap Stosch.

In East Greenland *Otoceras* is likewise a minor element of the fauna in contrast to *Ophiceras* (Tove Birkelund, personal communication). My own observations during a stay of approximately one month at Kap Stosch have confirmed this. Data are not available on the relative abundance of *Otoceras* and *Ophiceras* from northern Alaska, the Arctic Islands of Canada, Spitsbergen, and Siberia.

The Blind Fiord Formation of Ellesmere and Axel Heiberg Islands of Arctic Canada has yielded a fine sequence of faunas of lowermost Triassic age (Tozer, 1961, 1965, 1967). Four distinct zones have been recognized and brought together in a newly proposed stage, the Griesbachian. These zones and their included species are as follows (from bottom to top):

Concavum Zone
Otoceras concavum
Boreale Zone
Otoceras boreale
Metophiceras cf. *M. subdemissum*
Ophiceras sp. indet.
Commune Zone
Ophiceras commune
Ophiceras decipiens
Discophiceras wordiei
"Glyptophiceras" extremum
Strigatus Zone
Pachyproptychites strigatus
Ophiceras decipiens

A few comments are needed regarding the taxonomic usage adopted by Tozer (1967). It was mentioned above (p. 374) in the discussion of *Otoceras* that I consider *Otoceras concavum* nothing more than an intraspecific variant of *Otoceras woodwardi boreale*. Likewise, that *Metophiceras* is part of the ophiceratid radiation, and it is more consistent to consider it a subgenus of *Ophiceras*, as I also consider *Discophiceras* to be. The *Ophiceras decipiens* is equivalent to the *Vishnuites decipiens* Spath of East Greenland. Even though Tozer interpreted his species of *Ophiceras* very broadly, for which he is to be commended, the whole fauna is not as diverse as that of East Greenland and much less than that of the Himalayas.

It is the associations within each of these local zones that are of particular interest. *Otoceras* is restricted to the Concavum and Boreale Zones. It is the only genus of ammonoid known from the Concavum Zone. In the Boreale Zone, *Otoceras* is associated with *Ophiceras* of the *subdemissum* type and an indeterminant species. In addition, Tozer (1967: 53) records a "species of *Ophiceras* that has an acute venter" in a loose block containing specimens of *Otoceras boreale*. This I would interpret as a species of *Vishnuites*. Tozer (1967: 15) came to the conclusion that "exact correlatives of the Concavum Zone are not known," and that for the Boreale Zone "The presence of *Otoceras boreale* indicates a correlation with the Lower *Ophiceras* beds of East Greenland." It was pointed out above, however, that (a) *Otoceras concavum* is nothing more than an intraspecific variant of *Otoceras woodwardi boreale*, (b) that this species of *Otoceras* is present in the *Glyptophiceras* beds of East Greenland, and (c) it is also present in the Upper *Ophiceras* beds of East Greenland.

The Commune Zone contains *Ophiceras*, *Vishnuites*, and *Glyptophiceras*. The reason Tozer places quotes around *Glyptophiceras* is explained in a later paper (Tozer, 1969) and is of no particular concern here. This author then suggested that the Commune Zone of Arctic Canada, at least in its lower part, was correlative with the Upper *Ophiceras* beds of East Greenland. Tozer (1967: 16) commented further that: "the presence of *Ophiceras decipiens* [= *Vishnuites*] in the Commune Zone suggests that equivalents of the "*Vishnuites*" beds of East Greenland may also be present. A case might be made for recognizing a zone of *Ophiceras decipiens* between the Commune and Strigatus Zones in some sections, e. g. on Griesbach Creek. However, ophiceratids with acute venters that closely resemble *Ophiceras decipiens* occur as low as the Boreale Zone and this indicates that species of the *decipiens* group range through much of the Griesbachian."

In East Greenland *Ophiceras commune* is present in both the Lower and Upper *Ophiceras* beds, as is *Otoceras woodwardi boreale*. Also, as mentioned above, species of *Vishnuites* are present in the Upper *Ophiceras* beds.

In summary it can be seen that in most places *Otoceras* and *Ophiceras* occur together and that *Ophiceras* is by far the predominant form, *Otoceras* tending to be relatively rare. In the Himalayas the ranges of *Otoceras* and *Ophiceras* are the same at Painkhanda but not at Spiti. In the circum-Arctic region, for those regions where stratigraphic data are available, *Ophiceras* ranges stratigraphically higher than *Otoceras*. It would appear that for the circum-Arctic region the survival into the Lower Triassic (Scythian) was by no means the same from one locality to another. The Commune Zone of Arctic Canada does not contain *Otoceras*, but in East Greenland it does. In the eastern Verkhoyansk region *Ophiceras* ranges beyond *Otoceras*, but more data are needed on this section.

Thus, on the basis of available data, the lowest Scythian ammonoid zone is characterized by the predominance of *Ophiceras* and the much smaller presence of *Otoceras*. In most places the two genera occur together and thus cannot be used to mark two distinct biostratigraphic zones for purposes of intercontinental correlation. Separating the genera into two distinct zones for purposes of provincial correlation, as has been done in East Greenland and Arctic Canada, is quite acceptable, but this scheme breaks down when extended beyond these particular regions. The fact that even in the two principal areas of Triassic outcrops in the Himalayas (Spiti and Painkhanda) *Otoceras* is present throughout the range of *Ophiceras* in one locality but is confined to the lowermost bed in the other clearly demonstrates that the absence of *Otoceras* needs to be evaluated very carefully. More data are needed, but it appears that the present distributional pattern of *Otoceras* suggests that this genus became extinct in the Arctic region shortly after the beginning of the Triassic but persisted slightly longer in Tethys.

SYSTEMATIC SUMMARY OF OTOCERATIDAE

The Permian genera and species are listed from the writings of Ruzhentsev (1959, 1962, 1963) and Spinosa, Furnish, and Glenister (1970), with no attempt to evaluate either generic or specific taxa. The Triassic genera and species have been personally and carefully analyzed and represent my own personal assessment.

Genus *Araxoceras* Ruzhentsev, 1959

Type species, *A. latissimum* Ruzhentsev, 1959

A. latissimum Ruzhentsev, 1959: 58, figs. 1a, 2a; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 4.
A. trochoides (Abich), Ruzhentsev, 1959: 59.
A. latum Ruzhentsev, 1962: 90, pl. 1, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 5.
A. varicatum Ruzhentsev, 1962, pl. 4, fig. 2; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 6.
A. glenisteri Ruzhentsev, 1962, pl. 4, fig. 3; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 7.
A. rotoides Ruzhentsev, 1963: 57, pl. 5, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 2; Stepanov et al., 1969: 33, pl. 9, fig. 3.
A. tectum Ruzhentsev, 1963: 58, pl. 5, fig. 2; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 1.

Genus *Rotaraxoceras* Ruzhentsev, 1959

Type species, *R. caucasium* Ruzhentsev, 1959

R. caucasium Ruzhentsev, 1959: 61, figs. 1b, 2b; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 3.
R. deruptum Ruzhentsev, 1962: 93, pl. 4, fig. 4; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 4.

Genus *Prototoceras* Spath, 1930

Type species, *Ceratites tropitus* Abich, 1878 (= *Otoceras trochoides* Arthaber, non *Ceratites trochoides* Abich, 1878; = *Discotoceras* Spath, 1930).

P. tropitum (Abich) Abich, 1878: 13, pl. 2, fig. 3; pl. 11, fig. 21; Arthaber *in* Frech and Arthaber, 1900: 240; *Otoceras trochoides* Arthaber *in* Frech and Arthaber, 1900: 241, pl. 19, figs. 1–3; Ruzhentsev, 1959: 62, figs. 1c, 2c; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 6.

P. djoulfense (Abich), Abich, 1878: 11, pl. 2, fig. 1; pl. 11, fig. 20; Arthaber *in* Frech and Arthaber, 1900: 238; Ruzhentsev, 1959: 62.

P. intermedium (Abich), Abich, 1878: 12, pl. 2, fig. 4; Ruzhentsev, 1959: 62.

P. fedoroffi (Arthaber), Arthaber *in* Frech and Arthaber, 1900: 241, pl. 18, fig. 11; Ruzhentsev, 1959: 62.

P. discoidale Ruzhentsev, 1963: 58, pl. 5, fig. 3; pl. 6, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 7.

Genus *Urartoceras* Ruzhentsev, 1959

Type species, *U. abichanum* Ruzhentsev, 1959.

U. abichanum Ruzhentsev, 1959: 65, figs. 1g, 2g; Ruzhentsev, 1962: 94, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 5.

Genus *Pseudotoceras* Ruzhentsev, 1962

Type species, *P. armenorum* Ruzhentsev, 1962

P. armenorum Ruzhentsev, 1962, pl. 4, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 8.

P. djoulfense (Abich), Abich, 1878: 11, pl. 2, fig. 1; pl. 11, fig. 20; Ruzhentsev, 1963: 60, pl. 6, fig. 2; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 1; Stepanov et al., 1969, pl. 10, figs. 6, 7.

Genus *Vescotoceras* Ruzhentsev, 1962

Type species, *Prototoceras acutum* Ruzhentsev, 1959

V. acutum (Ruzhentsev), Ruzhentsev, 1959: 63, figs. 1d, 2d; Ruzhentsev, 1962: 96; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 2; Stepanov et al., 1969: 33, pl. 9, fig. 7.

V. parallelum (Ruzhentsev), Ruzhentsev, 1959: 63, figs. 1e, 2e; Ruzhentsev, 1962: 97; Ruzhentsev and Sarycheva, 1965, pl. 19, figs. 3, 4; Stepanov et al., 1969: 33, pl. 9, fig. 5.

V. pessoides (Abich), Abich, 1878: 15, pl. 1, fig. 5; Arthaber *in* Frech and Arthaber, 1900: 235, pl. 18, fig. 9; Ruzhentsev, 1959: 63; Ruzhentsev, 1962: 97.

V. serratum Ruzhentsev, 1962: 97, pl. 4, fig. 6.

V. eranidum Ruzhentsev, 1962: 97, pl. 4, fig. 7; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 5.

Genus *Dzhulfoceras* Ruzhentsev, 1962

Type species, *D. furnishi* Ruzhentsev, 1962

D. furnishi Ruzhentsev, 1962: 99, pl. 5, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 6.

D. paulum Ruzhentsev, 1962: 99, pl. 5, fig. 2.

D. inflatum Ruzhentsev, 1963: 61, pl. 5, fig. 4; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 7.

Genus *Vedioceras* Ruzhentsev, 1962

Type species, *V. ventroplanum* Ruzhentsev, 1962

V. ventroplanum Ruzhentsev, 1962: 100, pl. 5, fig. 3; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 1; Stepanov et al., 1969: 33, pl. 9, fig. 6.

V. ogbinense Ruzhentsev, 1962: 102, pl. 5, fig. 4.

V. umbonovarum Ruzhentsev, 1963: 62, pl. 5, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 2; Stepanov et al., 1969: 33.

V. ventrosulcatum Ruzhentsev, 1963: 63, pl. 5, fig. 6; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 3.

Genus *Avushoceras* Ruzhentsev, 1962

Type species, *A. jakowlewi* Ruzhentsev, 1962

A. jakowlewi Ruzhentsev, 1962: 103, pl. 5, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 4; Stepanov et al., 1969: 33.

Genus *Eoaraxoceras* Spinosa, Furnish, and Glenister, 1970

Type species, *E. ruzhencevi* Spinosa, Furnish, and Glenister, 1970.

E. ruzhencevi Spinosa, Furnish, and Glenister, 1970: 732, pl. 109, figs. 1–9.

Genus *Anotoceras* Hyatt, 1900

Type species, *Prosphingites nala* Diener, 1897.

A. nala (Diener), Diener, 1897: 54, pl. 1, fig. 4; pl. 7, fig. 13; Hyatt, 1900: 553; von Krafft and Diener, 1909: 159; Diener, 1915: 233; Spath, 1930: 7, 8; Spath, 1934: 70, figs. 12a, b; Kummel *in* Arkell et al., 1957: L132, figs. 162, 7a, b; Ruzhentsev, 1959: 66.

Prosphingites kama Diener, 1897: 56, pl. 1, fig. 5; Diener, 1915: 233; Spath, 1934: 70, fig. 12c.

Anotoceras intermedium Spath, 1930: 8; Spath, 1934: 70.

Genus *Otoceras* Griesbach, 1880

Type species, *Otoceras woodwardi* Griesbach, 1880

Subspecies *Otoceras woodwardi woodwardi* Griesbach

Otoceras woodwardi Griesbach, 1880: 106, pl. 1, figs. 4, 5; pl. 2, figs. 1–6; Frech, 1901: 575, figs. 4a–d; Frech, 1902: 628, 629; von Krafft and Diener, 1909: 116; Diener, 1915: 213; Diener, 1925: 34, pl. 22, fig. 1; Spath, 1930: 9–11; Spath, 1934: 66, fig. 10; Spath, 1935: 11; Kummel *in* Arkell et al., 1957: L132, fig. 162, 10.

Hungarites (*Otoceras*) *woodwardi*, –Diener, 1897: 156–160, pl. 2, fig. 1; pl. 3, fig. 1; pl. 4, figs. 2, 4, 5; pl. 5, figs. 1, 3, 5; pl. 6, fig. 16.

Otoceras woodwardi var. *undatum* Griesbach, 1880: 107, pl. 1, fig. 5.

Hungarites (*Otoceras*) *undatum*, –Diener, 1897: 162, pl. 4, fig. 6.

Otoceras undatum, –Diener, 1915: 213; Spath, 1934: 69.

Otoceras cf. *undatum*, –von Krafft and Diener, 1909: 116.

Hungarites (*Otoceras*) *parbati* Diener, 1897: 160, pl. 4, fig. 1.

Otoceras parbati Diener, 1915: 213.

Otoceras clivei Diener, 1897: 161, pl. 3, figs. 2, 4; pl. 5, fig. 4; pl. 7, fig. 17; von Krafft and Diener, 1909: 116; Diener, 1915: 213; Nakazawa et al., 1970, pl. 28, figs. 1a–c.

Otoceras nov. sp. ind. aff. *clivei* Diener *in* von Krafft and Diener, 1909: 116, pl. 29, fig. 3; Diener, 1915: 213.

Hungarites (*Otoceras*) *fissisellatum* Diener, 1897: 163, pl. 3, fig. 3; pl. 5, fig. 2.

Otoceras fissisellatum Diener, 1915: 213; Spath, 1930: 10.

Hungarites (*Otoceras*) *draupadi* Diener, 1897: 164, pl. 4, fig. 3; pl. 5, fig. 6; pl. 7, fig. 15.

Otoceras draupadi Diener, 1915: 213; Nakazawa et al., 1970, pl. 28, figs. 3a, b.

Hungarites sp. indet. Diener, 1897: 150, pl. 23, fig. 5; Diener, 1915: 154.

Otoceras (*Metotoceras*) *dieneri* Spath, 1930: 8; Spath, 1934: 69; Kummel *in* Arkell et al., 1957: L132.

Subspecies *Otoceras woodwardi boreale* Spath, 1935

Type species, *Otoceras boreale* Spath, 1935

Otoceras aff. *fissisellatum*, Spath, 1930: 10–12, pl. 1, figs. 1a–d; Koch, 1931: 79; Spath, 1934: 68.

Otoceras boreale Spath, 1935: 9–11, pl. 1, figs. 1a, b, 6; pl. 2, figs. 2, 3; pl. 3, figs. 1–3; pl. 4, fig. 1; pl. 5, fig. 1; pl. 6, fig. 8; Kummel *in* Reeside et al., 1957: 1501; Popov, 1958: 107, text-figs. 1, 2 (A.G.I. translation, 1960); Popov, 1961: 20–22, pl. 3, figs. 4, 5; Tozer, 1961: 45–47, pl. 6, figs. 1a–3; pl. 7, figs. 1–3b; pl. 8, figs. 1–4b; Keller et al., 1961: 187; Trümpy, 1961: 249; Vozin and Tikhomirova, 1964: 47, pl. 25, figs. 1a, b; Trümpy, 1969: 83.

Otoceras indigirense Popov, 1958: 109, text-figs. 1a, 2a, b; Popov, 1961: 22, pl. 1, fig. 3.

Otoceras sp. indet. Petrenko, 1963: 51, pl. 1, fig. 1.

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Plate 1. *Otoceras woodwardi woodwardi*

Figures 1–12. *Otoceras woodwardi woodwardi* Griesbach 391

1, 2. Lectotype (Griesbach, 1880, pl. 1, fig. 4; Diener, 1897, pl. 4, fig. 2) GSI 5930. × 1.

3, 4. Paralectotype (Griesbach, 1880, pl. 2, fig. 2; Diener, 1897, pl. 4, fig. 4) GSI 5932. × 1.

5, 6. Topotype (Diener, 1897, pl. 5, fig. 3) GSI 5937. × 1.

7, 8. Small, juvenile specimen, in same tray as Griesbach's lectotype (GSI 5930). × 3.

9, 10. Topotype (Diener, 1897, pl. 5, fig. 5) GSI 5939. × 1.

11, 12. Topotype (Diener, 1897, pl. 4, fig. 5) GSI 5933. × 1.

All specimens from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhanda, Niti region, Himalayas, India.

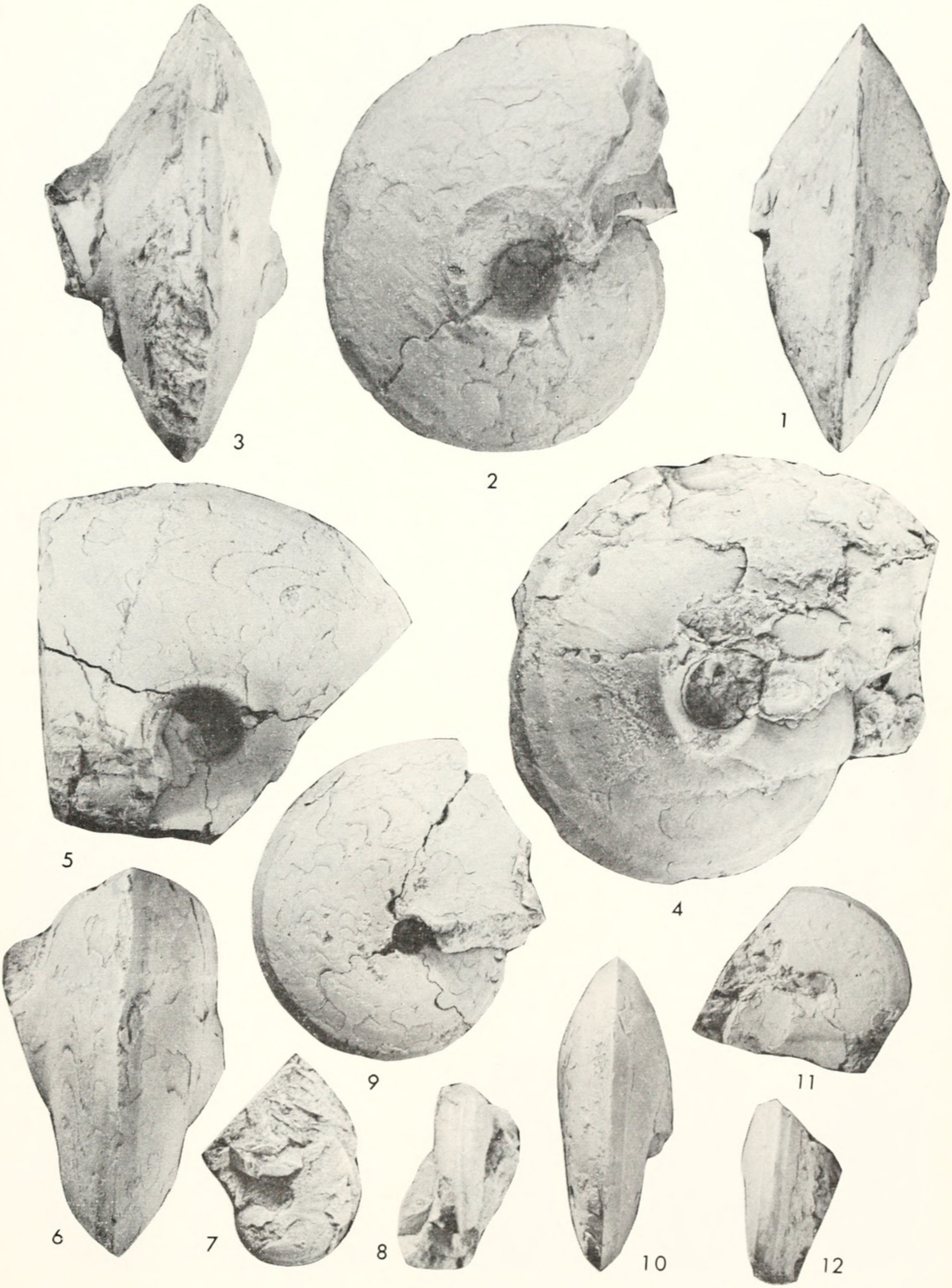
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Plate 2. *Otoceras woodwardi woodwardi*

Figures 1–15. *Otoceras woodwardi woodwardi* Griesbach 391

1, 2. Topotype (Diener, 1897, pl. 3, fig. 1) GSI 5925. × $\frac{2}{3}$.
3, 4. Topotype (Diener, 1897, pl. 2, fig. 1) GSI 5924. × $\frac{1}{2}$.
5–7. Topotype, BM(NH) 28512. × $1\frac{1}{2}$.
8–10. Topotype, BM(NH) 28514. × 3.
11, 12. Topotype, BM(NH) 28513a. × 4.
13–15. Topotype, BM(NH) 28513b. × 8.

All specimens from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhanda, Niti region, Himalayas, India.

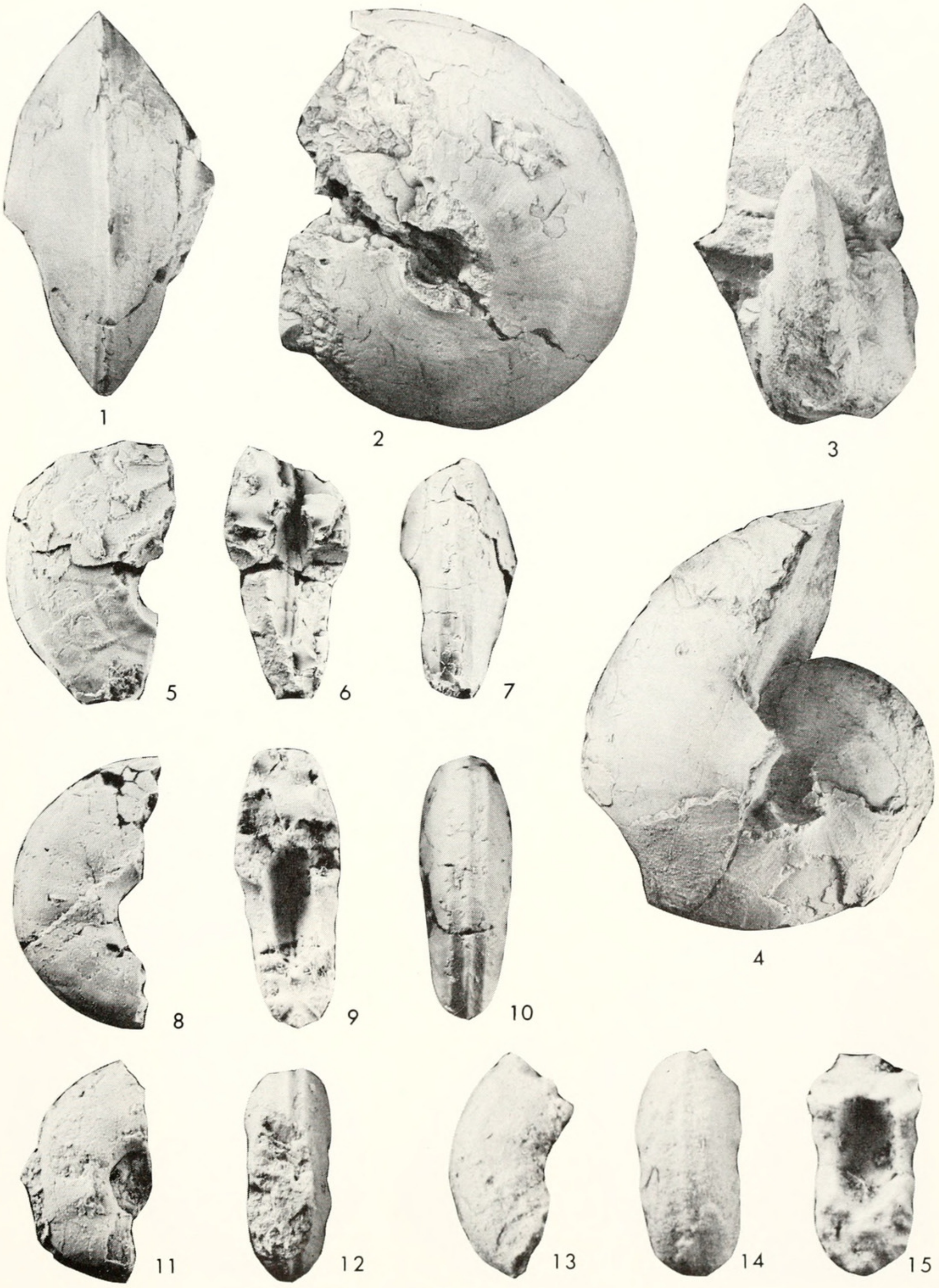
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Plate 3. *Otoceras woodwardi woodwardi*

1, 2. Syntype, *Otoceras clivei* Diener (1897, pl. 3, fig. 4) GSI 5928. × 1.

3, 4. Holotype, *Otoceras* (*Metotoceras*) *dieneri* Spath (1950: 8) = *Hungarites* sp. ind. Diener (1897: 150, pl. 23, fig. 5) GSI 6058. × 1.

5, 6. Syntype, *Otoceras clivei* Diener (1897, pl. 5, fig. 4) GSI 5938. × 1.

7, 8. Syntype, *Otoceras clivei* Diener (1897, pl. 3, fig. 2) GSI 5926. × 1.

9, 10. Holotype, *Otoceras woodwardi* var. *undatum* Griesbach (1880, pl. 1, fig. 5) GSI 5934. × 1.

11. Suture specimen of *Otoceras clivei* (Diener, 1897, pl. 7, fig. 17) GSI 5964. × 1.

12. Suture specimen of *Otoceras woodwardi* (Diener, 1897, pl. 7, fig. 16) GSI 5963. × 1.

All specimens from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhanda, Niti region, Himalayas, India.

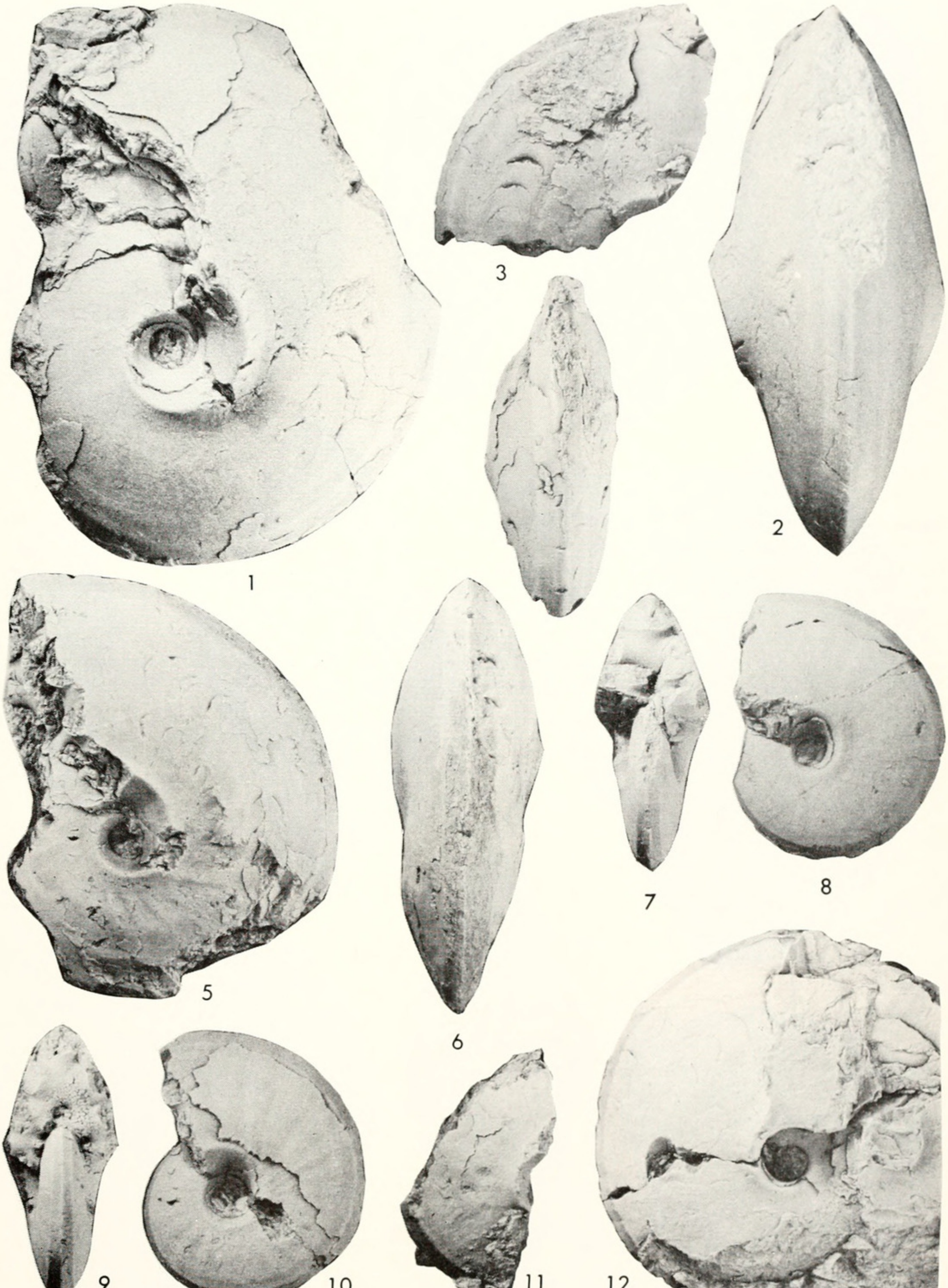
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Plate 4. *Otoceras woodwardi woodwardi*

Figures 1–10. *Otoceras woodwardi woodwardi* Griesbach 391

1, 2. Syntype, *Otoceras draupadi* Diener (1897, pl. 4, fig. 3) GSI 5931. × 1.

3, 4. Suture specimen of *Otoceras draupadi* Diener (1897, pl. 5, fig. 6) GSI 5940. × 1.

5, 6. Suture specimen of *Otoceras draupadi* Diener (1897, pl. 7, fig. 15) GSI 5962. × 1.

7, 8. Paralectotype, *Otoceras fissisellatum* Diener (1897, pl. 5, fig. 2) GSI 5936. × 1.

9, 10. Holotype, *Otoceras parbati* Diener (1897, pl. 4, fig. 1) GSI 5929. × 1.

Specimens of figures 1–8 from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhanda, Niti region, Himalayas, India. Specimen of figures 9, 10 from *Otoceras* beds, Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.


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Plate 5. *Ophiceras tibeticum*

Figures 1–10. *Ophiceras tibeticum* Griesbach 384

1, 2. Lectotype (Griesbach, 1880, pl. 3, fig. 4; Diener, 1897, pl. 8, fig. 1) GSI 5965. × 1.

3, 4. Plesiotype (Diener, 1897, pl. 8, fig. 2) GSI 5966. × 1.

5, 6. Plesiotype (Diener, 1897, pl. 8, fig. 5) GSI 5969. × 1.

7, 8. Plesiotype (Diener, 1897, pl. 8, fig. 6) GSI 5970. × 1.

9, 10. Plesiotype (Diener, 1897, pl. 8, fig. 3) GSI 5967. × 1.

Specimen of figures 1, 2 from *Otoceras* beds at Shalshal Cliff near Rimkin Paiar encamping ground, those of figures 3–10 from Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.


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Plate 6. *Ophiceras serpentinum*

Figures 1–12. *Ophiceras serpentium* Griesbach 384

1, 2. Paralectotype (Diener, 1897, pl. 13, fig. 4) GSI 6002. × 1.
3, 4. Paralectotype (Diener, 1897, pl. 13, fig. 5) GSI 6003. × 1.
5, 6. Paralectotype (Diener, 1897, pl. 13, fig. 6) GSI 6004. × 1.
7, 8. Paralectotype (Diener, 1897, pl. 13, fig. 1) GSI 5999. × 1.
9, 10. Paralectotype (Diener, 1897, pl. 13, fig. 7) GSI 6005. × 1.
11, 12. Paralectotype (Diener, 1897, pl. 13, fig. 3) GSI 6001. × 1.

All specimens from *Otoceras* beds of Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.


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Plate 7. *Ophiceras medium*

Figures 1–13. *Ophiceras medium* Griesbach 384

1, 2. Syntype, *Ophiceras platyspira* (Diener, 1897, pl. 12. fig. 6) GSI 5998. × 1.

3, 4. Syntype, *Ophiceras platyspira* (Diener, 1897, pl. 12, fig. 5) GSI 5997. × 1.

5, 6. Paralectotype, *Ophiceras chamunda* (Diener, 1897, pl. 12, fig. 1) GSI 5993. × 1.

7, 8. Paratype (Diener, 1897, pl. 9, fig. 1) GSI 5972. × 1.

9. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 1) GSI 6006. × 1.

10, 11. Lectotype, *Ophiceras chamunda* (Diener, 1897, pl. 12, fig. 3) GSI 5995. × 1.

12, 13. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 2) GSI 6007. × 1.

Specimens of figures 1–6, 10, 11 from *Otoceras* beds at Rimkin Paiar encamping ground, Shalshal Cliff, and those of figures 7–9, 12, 13 from Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.


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Plate 8. *Ophiceras medium*

Figures 1–16. *Ophiceras medium* Griesbach 384

1, 2. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 7) GSI 5978. × 1.

3, 4. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 6) GSI 5977. × 1.

5, 6, 7. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 3) GSI 5974. × 1.

8, 9. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 5) GSI 5976. × 1.

10–12. Holotype, *Ophiceras gibbosum* (Griesbach, 1880, pl. 3, fig. 10; Diener, 1897, pl. 9, fig. 4) GSI 5975. × 1.

13, 14. Paralectotype, *Ophiceras chamunda* (Diener, 1897, pl. 12, fig. 2) GSI 5994. × 1.

15, 16. Holotype (Griesbach, 1880, pl. 3, fig. 9; Diener, 1897, pl. 9, fig. 2) GSI 5973. × 1.

Specimens of figures 1–16 from *Otoceras* beds at Rimkin Paiar encamping ground, Shalshal Cliff, Painkhanda, Niti region, Himalayas, India.

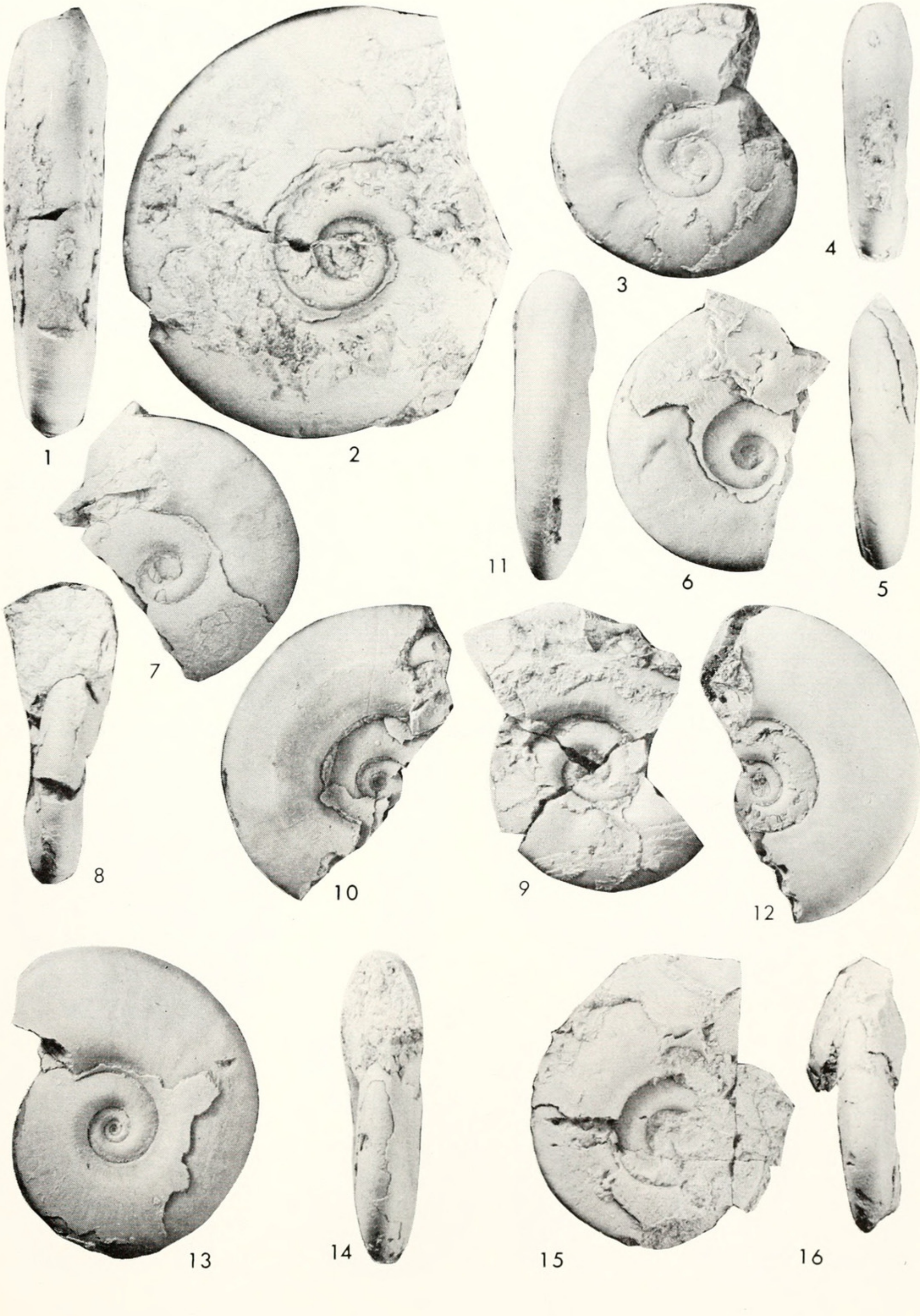

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Plate 9. *Ophiceras medium*

Figures 1–14. *Ophiceras medium* Griesbach 384

1, 2. Lectotype, *Ophiceras ptychodes* (Diener, 1897, pl. 11, fig. 5) GSI 5991. × 1.
3, 4. Paralectotype, *Ophiceras ptychodes* (Diener, 1897, pl. 11, fig. 6) GSI 5992. × 1.
5, 6. Paralectotype, *Ophiceras ptychodes* (Diener, 1897, pl. 11, fig. 3) GSI 5989. × 1.
7, 8. Lectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 1) GSI 5979. × 2/3.
9, 10. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 3) GSI 6008. × 1.
11, 12. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 6) GSI 6011. × 2.
13, 14. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 7) GSI 6010. × 2.

Figure 15. *Ophiceras tibeticum* Griesbach 384

Lectotype, *Ophiceras serpentinum* Diener (1897, pl. 13, fig. 2) GSI 6000. × 1.

Specimens of figures 1–8, 11, 12 from *Otoceras* beds, Rimkin Paiar encamping ground, Shalshal Cliff, those of figures 9, 10, 15 from Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India; specimens of figures 13, 14 from Tengdi, Spiti, Himalayas, India.

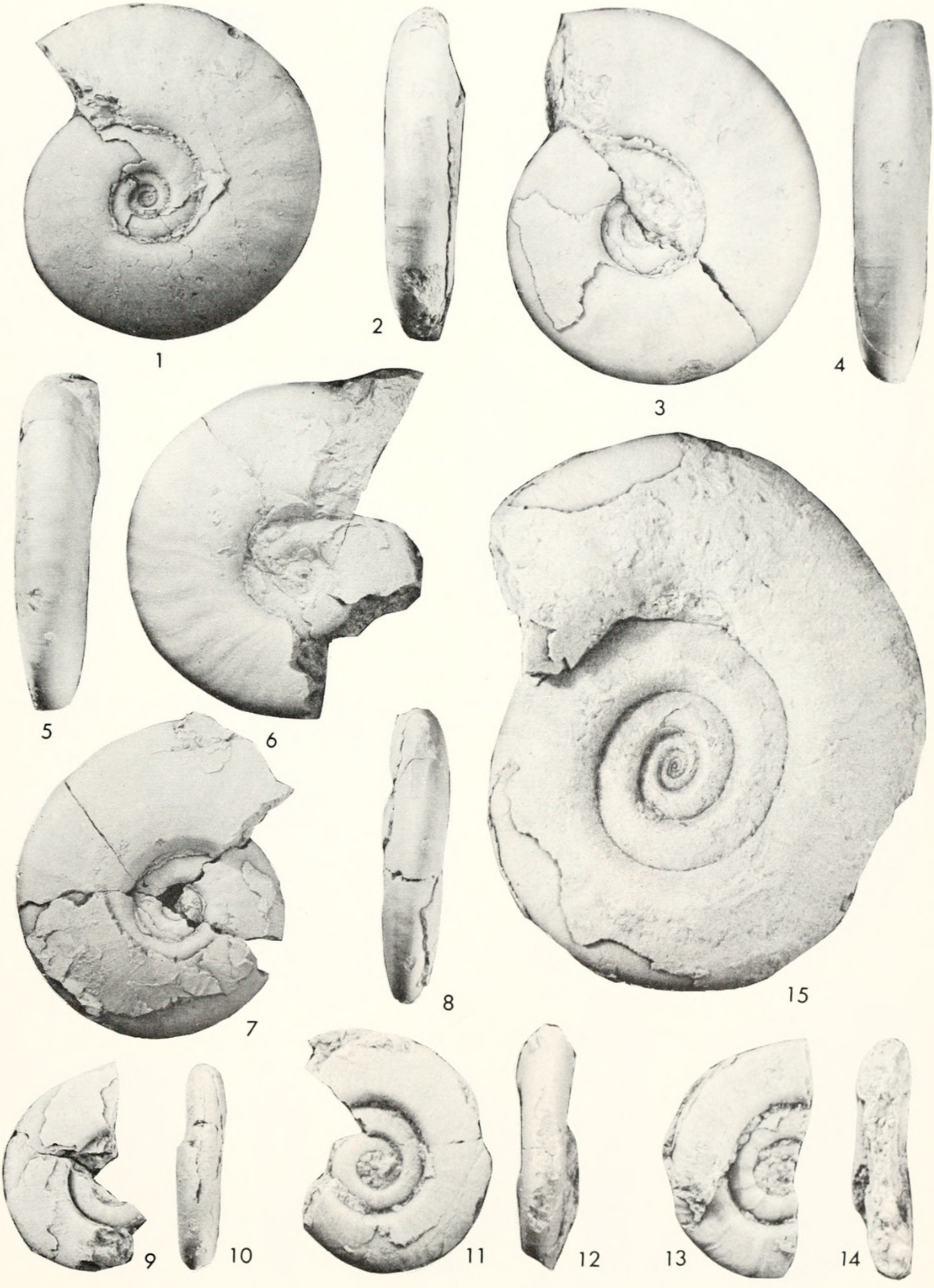
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Plate 10. *Ophiceras medium*

Figures 1–18. *Ophiceras medium* Griesbach 384

1, 2. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 11, fig. 4) GSI 5990. × 1.
3, 4. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 11, fig. 2) GSI 5988. × 1.
5, 6. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 11, fig. 1) GSI 5987. × 1.
7, 8. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 7) GSI 5985. × 2.
9, 10. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 6) GSI 5984. × 1.
11, 12. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 8) GSI 5986. × 1.
13, 14. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 5) GSI 5983. × 1.
15, 16. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 3) GSI 5981. × 1.
17, 18. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 2) GSI 5980. × 1.

Specimen of figures 7, 8 from *Otoceras* beds southeast of Muth, Spiti, all the remaining specimens from same horizon at Rimkin Paiar encamping ground, Shalshal Cliff, Painkhanda, Niti region, Himalayas, India.


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Plate 11. *Episageceras, Proptychites, Glyptophiceras*

Figures 1–4. *Episageceras dalailamae* (Diener) 381

1, 2. Holotype (Diener, 1897, pl. 1, fig. 6) GSI 5922. × 1.
3, 4. Paratype (Diener, 1897, pl. 7, fig. 7) GSI 5953. × 1.

Figures 5, 6. *Proptychites scheibleri* Diener 382

Holotype (Diener, 1897, pl. 6, fig. 3) GSI 5943. × 1.

Figure 7. *Glyptophiceras himalayanum* (Griesbach) 382

Holotype (Griesbach, 1880, pl. 3, fig. 8; Diener, 1897, pl. 14, fig. 14) GSI 6019. × 1.
Upper specimen is *Otoceras woodwardi*.

All specimens from *Otoceras* beds at Rimkin Paiar encamping ground, Shalshal Cliff, Painkhanda, Niti region, Himalayas, India.

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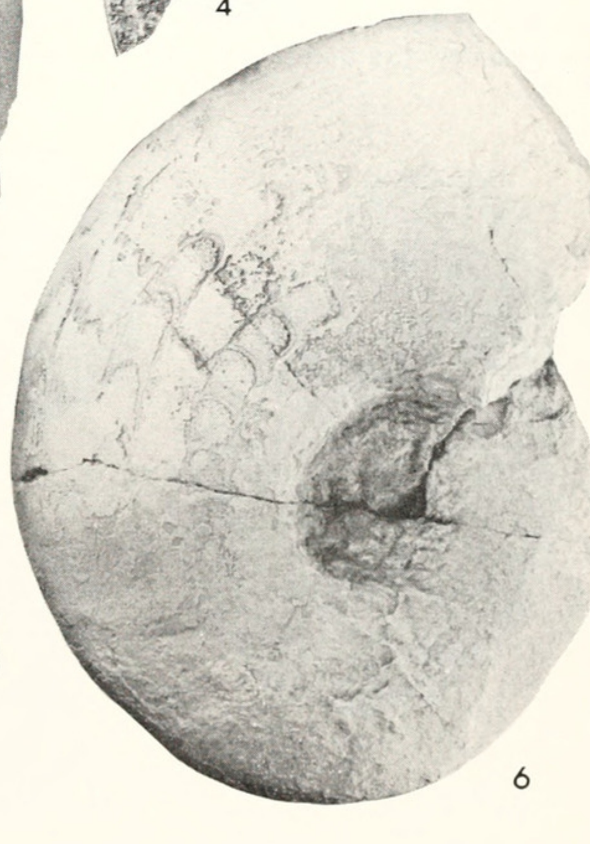

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Plate 12. *Vishnuites, Prionolobus, Anotoceras,* and "*Xenodiscus*"

Figures 1–4. *Vishnuites pralambha* Diener 382

1–3. Holotype (Diener, 1897, pl. 7, fig. 4) GSI 5950. × 1.
4. Paratype (Diener, 1897, pl. 7, fig. 5) GSI 5951. × 1.

Figures 5–8. *Prionolobus hodgsoni* (Diener) 382

5, 6. Holotype (Diener, 1897, pl. 6, fig. 1) GSI 5941. × 1.
7, 8. Topotype (v. Krafft and Diener, 1909, pl. 30, fig. 1) GSI 9537. × 1

Figures 9–14. *Anotoceras nala* (Diener) 379

9, 10. Paralectotype (Diener, 1897, pl. 7, fig. 13) GSI 5959. × 1.
11, 12. Lectotype (Diener, 1897, pl. 1, fig. 4) GSI 5920. × 1.
13, 14. Holotype, *Prosphingites kama* Diener (1897, pl. 1, fig. 5) GSI 5921. × 1.

Figure 15. "*Xenodiscus*" *radians* von Krafft (non Waagen) 383

Illustrated in von Krafft and Diener (1909, pl. 25, fig. 2) GSI 9504. × 1.

Specimens of figures 1–8 from *Otoceras* beds, Rimkin Paiar encamping ground, Shalshal Cliff, those of figures 9–14 from Kiunglung encamping ground, Painkhanda, Niti region; that of figure 15 from *Otoceras* beds, Lilang, Spiti region, Himalayas, India.


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